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JOURNAL OF ANATOMY

THE NERVE SUPPLY OF THE INTERPHALANGEAL AND METACARPO-PHALANGEAL JOINTS

By JOHN S. B. STOPFORD, M.D.,
Professor of Anatomy, University of Manchester

The numerous examples of injuries, incurred during the war, to the peripheral nerves have offered us a unique opportunity of studying the distribution of these nerves from a functional aspect, and consequently of widely supplementing a knowledge which had been obtained chiefly by dissection. The most careful and deliberate dissections of the peripheral nerves fail to provide information about the function of the constituent fibres, and yet it is exactly this knowledge which is often most urgently required in the clinical investigation of a patient.

In this paper it is my endeavour to describe the distribution to the interphalangeal and metacarpo-phalangeal joints of the thumb and fingers of the nerve fibres which conduct sensory impressions that determine a consciousness of passive movement, and impulses which enable us to recognise posture. It will become obvious that such investigations as are described in this paper cannot possibly give any information about those fibres which conduct from the joints to the cerebellum impulses, which of course make no appeal to consciousness.

A precise knowledge of this subject is fundamental for any research upon sensation, is also of considerable importance for the purposes of diagnosis and prognosis and is becoming of increasing significance in the late treatment of peripheral nerve injuries by methods of muscle re-education and training (1).

The patients selected for this investigation were those in which definite peripheral nerves of the upper extremity were known to be completely severed, and in which there was no complication such as division of tendons or any limitation of mobility in the joints; since it has been proved clinically that a number of afferent fibres subserving the recognition of pressure reach their distribution by such structures as tendons, and of course any limitation of movement of the joints would interfere seriously with the performance of the tests.

The examination was first made on the normal side in order to make the patient quite familiar with the method and what was expected of him, secondly to provide a control and standard for comparison, and thirdly to enable me to test the reliability and attention of the patient. It is surprising how few patients need to be discarded as unreliable if sufficient time is taken to make

quite clear to them what is wanted and enough patience is expended. A large number of patients, who were otherwise quite suitable, had to be omitted on account of arthritic adhesions, a complication unfortunately very frequently encountered in peripheral nerve lesions. Each segment of the digit, above and below the joint to be examined, was grasped firmly by the lateral borders and then the joint was gradually and evenly flexed or extended. The segments of the digit must be grasped firmly, as Head(2) has pointed out, so that the additional pressure required to move the joint shall not be distinguishable and thus lead to the recognition of movement from other impressions than those arising from the articular structures. The movement of the joint must also be made as far as possible at a uniform rate and not too slowly.

The patient was requested to state when he first felt any movement, and on answering was further asked at which joint it occurred and also the apparent direction of the movement. The latter two questions were soon found to be of fundamental importance for any accurate investigation of the appreciation of passive movement in a *joint*, since it was found that patients were able frequently to recognise movement of a particular digit without possessing any knowledge of the joint at which it occurred or the direction in which it was moved. Investigation of the earlier cases showed that this recognition of mere movement of a digit was obviously dependent upon alteration in tension or position of the tendons, and did not arise from any stimulation of afferent nerve terminals in the region of the joint. Fortunately this source of fallacy was discovered at an early stage in the investigation, and errors arising from it were consequently prevented. From a review of other work on this aspect of sensation it seems possible that fallacies may have arisen in the past from this cause. Another source of possible error which was soon discovered arose from the difficulty patients had in expressing the joint at which the movement was experienced. Such a term as the "first joint" is apt to be very misleading, as some referred this to the proximal interphalangeal joint and others to the distal: consequently it was found necessary at the outset of each examination to have a clear understanding with the patient as to the terminology he adopted for the various joints. In all, 51 patients have been examined and they are composed of the following and will be considered in this order:

Division of ulnar ... ... 20 (in arm 5, in forearm 11, at wrist 4).
Division of median ... ... 12 (in arm 5, in forearm 5, at wrist 2).
Division of musculo-spiral ... 14.
Division of median and ulnar 4 (in forearm 3, at wrist 1).
Division of median and radial 1 (in forearm).

For greater ease of comparison the left hand is represented in all the figures.

ULNAR NERVE

In all 20 an absolute loss of all appreciation of passive movement was found in the two interphalangeal joints and the metacarpo-phalangeal joint of the little finger, but the extent of the supply from the ulnar to the articula-

tions of the ring finger was subject to considerable variation. In eight the power of perception of movement in all three joints of the ring finger was definitely impaired (fig. 1 *A*), and this was particularly striking on comparing the same joint on the two sides. In one of the eight in addition there was also defective recognition of movement at the metacarpo-phalangeal joint of the middle finger (fig. 1 *B*). Four other patients failed to recognise any movement at the two interphalangeal joints of the ring finger, in three of these a defect was also found at the metacarpo-phalangeal joint of the same finger (fig. 1 *C*), and in

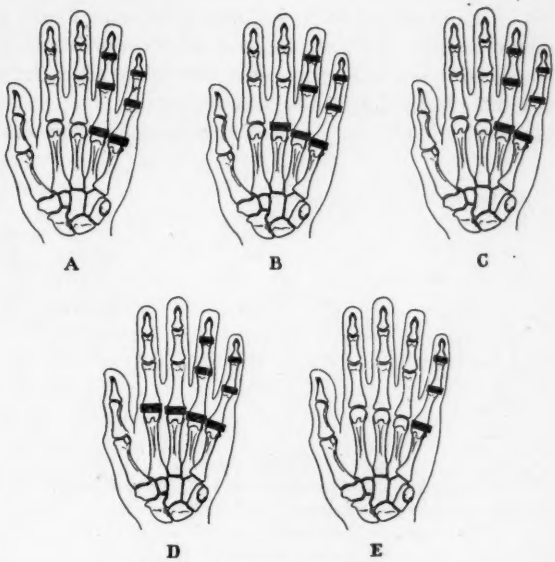

Fig. 1. Division of ulnar nerve.
■ = Complete loss of appreciation of passive movement.
▬ = Impaired recognition of passive movement.
Type *A* = 7 patients. Type *D* = 1 patient.
„ *B* = 1 patient. „ *E* = 5 patients.
„ *C* = 3 patients.

the fourth a similar defect at the metacarpo-phalangeal joint of the ring, middle and index fingers (fig. 1 *D*). In five no objective or subjective evidence of any ulnar supply to any joint of the ring finger could be demonstrated (fig. 1 *E*). This accounts for 17 out of the 20, the condition found in the remaining three is shown in fig. 2, *A*, *B* and *C*.

The explanation of the variation in distribution of the ulnar to the joints of the ring finger is readily appreciated on reference being made to the variation already described in the cutaneous distribution of this nerve (3), since it was discovered that a more profound loss of the appreciation of movement was present in those patients where the supply to the skin of the fingers was found

to be more extensive than that usually described. A very intimate and significant relation between the extent of the distribution to the joints and the skin of the fingers was discovered throughout this series.

The supply to the metacarpo-phalangeal joint of the index in one patient could not be explained in this way and it must be consequently presumed that the distribution to this joint, in the one patient, was through the deep palmar branch.

It is of the greatest importance to notice that no modification in distribution to the articulations of the fingers was produced by section of the nerve at different levels in the limb, precisely similar results being found whether the nerve was severed in the upper arm, forearm or at the wrist; fuller reference to the significance of this will be made at a later stage after the distribution of the various nerves to the joints has been discussed.

From these results it may be deduced that normally the ulnar conducts

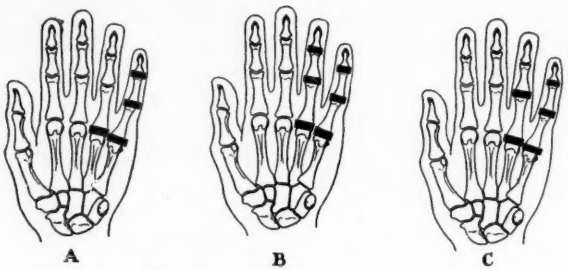

Fig. 2. Division of ulnar nerve.
■ = Complete loss of appreciation of passive movement.
▩ = Impaired recognition of passive movement.
One patient showing each type = *A*, *B* and *C*.

afferent impulses that excite consciousness from all the three joints of both the little and ring fingers, it invariably provides the sole pathway in the case of the former, but in the latter finger considerable variation is found; broadly speaking in most people it provides the principal course for the transmission of impulses from the three articulations of the ring finger.

MEDIAN NERVE

Most variation in the median distribution was discovered in the supply to the joints of the thumb (fig. 3), and the reason for this will be quite apparent after we have considered the distribution of the radial. Only in one patient out of the twelve examined was no impairment of the perception of movement found in the two joints of the thumb. Two patients were unable to recognise any movement of either joint, and in two others the power of appreciation of movement was definitely diminished in the two joints. In the remaining seven the condition in the two articulations of the thumb differed. In four defective

recognition, and in another complete loss, was found in the interphalangeal joint, whereas the metacarpo-phalangeal was unaffected; in the other two there was failure to recognise movement in the interphalangeal joint and some disturbance at the metacarpo-phalangeal joint.

Loss of appreciation of movement in both interphalangeal joints of the index and medius was the rule in all twelve; complete failure to recognise movement in any joint of the index was discovered in four and a similar condition in the medius in six. Of the remaining eight, as regards the metacarpo-

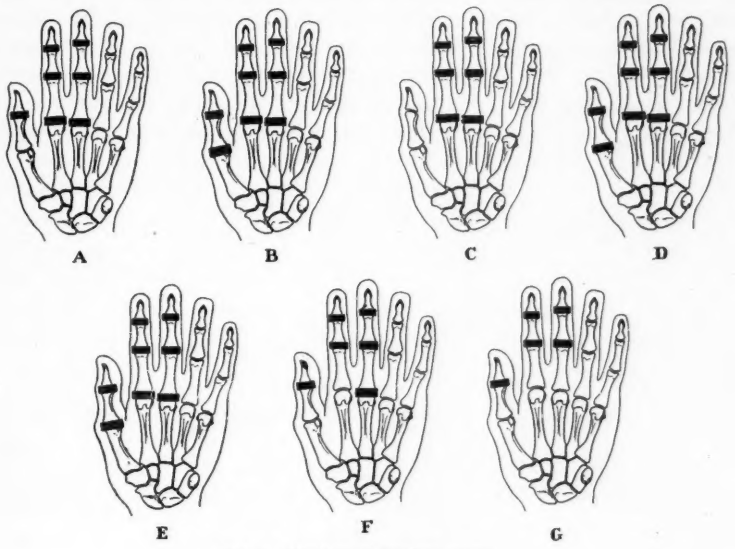

Fig. 3. Division of median nerve.
■ = Complete loss of appreciation of passive movement.
▩ = Impaired recognition of passive movement.

Type A = 4 patients.	Type E = 1 patient.
„ B = 1 patient.	„ F = 1 patient.
„ C = 1 patient.	„ G = 2 patients.
„ D = 2 patients.	

phalangeal joint of the index, five manifested imperfect perception and three showed no clinical evidence of any distribution to this joint from the median. Of the six, which remain to be considered with reference to the metacarpo-phalangeal joint of the middle finger, four showed imperfect perception and in two no disturbance could be detected.

In no patient was I able to discover any subjective or objective sign of any distribution from the median to the articulations of the ring finger, although the results found after division of the ulnar anticipate some evidence to this effect, but it must be remembered that we decided that the ulnar appeared to provide the principal supply to the joints of this finger. Consequently it seems

probable that in the 12 patients examined the ulnar provided the main supply to the joints of the ring finger, and the distribution from the median was insufficient to be appreciated by clinical tests.

From these results it appears that the median normally provides the sole pathway for the transmission of afferent impulses from both interphalangeal joints of the index and medius fingers, is the principal pathway from the metacarpo-phalangeal joints of these two fingers and the interphalangeal joint of the thumb, and provides frequently a route for the passage of these impulses from the metacarpo-phalangeal joint of the thumb. We have no direct evidence from the examination of these 12 patients, but it may be surmised that the median supplements the distribution of the ulnar to the articulation of the ring finger.

The fact must be again emphasised that the level of division of the nerve in the limb did not in any way control the extent of the distribution of afferent fibres conveying sensory impressions from the joints.

MUSCULO-SPIRAL NERVE

Fourteen patients were examined in which this nerve had been severed, but of course the study of these patients really resolves itself into an investigation

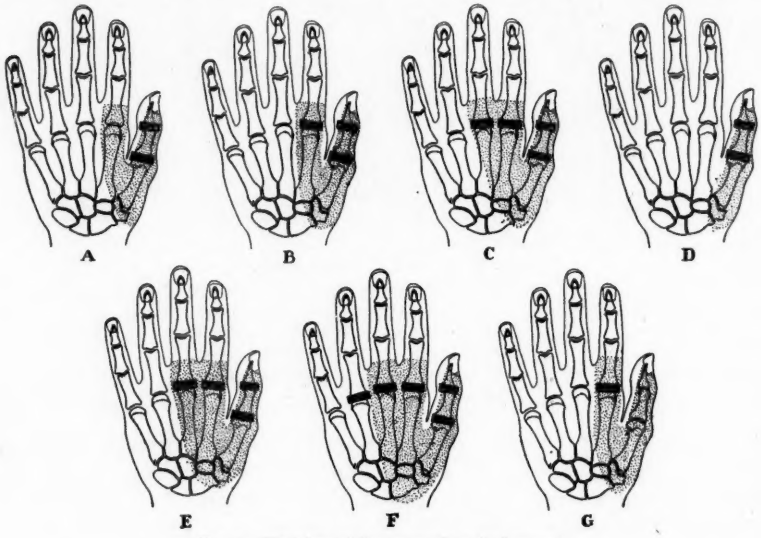

Fig. 4. Division of the musculo-spiral nerve.
■ = Complete loss of appreciation of passive movement.
▨ = Impaired recognition of passive movement.
◉ = Extent of anaesthesia to lightest possible stimulations.

Type *A* = 1 patient.
„ *B* = 4 patients.
„ *C* = 3 patients.
„ *D* = 1 patient.
Type *E* = 1 patient.
„ *F* = 1 patient.
„ *G* = 1 patient.

of the distribution of the radial and lower external cutaneous branches of the musculo-spiral to the joints.

In two the recognition of passive movements appeared to be perfect in all the joints, but in the remainder one or more articulations of the thumb or fingers were affected, and the extent of this distribution was found to be subject to considerable variation. It is of interest to remember that there was no disturbance of the perception of passive movement in Head's historical experiment (4), upon which depends a good deal of our present conception of deep sensibility; and it seems possible from the fact that a similar result was found in only two patients out of 14 that this form of distribution is the exception rather than the rule.

The simplest way of demonstrating the disturbances found in this series has been to represent the conditions found in the 12 patients graphically in fig. 4. As in the case of the ulnar a close relationship was maintained between the extent of the distribution of the radial to the skin and to the joints. The results also explain quite definitely the variations which have been described in the distribution of the median to the two joints of the thumb and the metacarpo-phalangeal joints of the index and middle fingers. The investigation has proved that the radial as a rule supplements the supply of the median to the two joints of the thumb (frequently providing the chief supply to the metacarpo-phalangeal joint of the thumb), and the metacarpo-phalangeal joint of the index; the radial may be the sole supply to the metacarpo-phalangeal joint of the thumb and not infrequently supplements the median distribution to the metacarpo-phalangeal joint of the middle finger.

MEDIAN AND ULNAR NERVES

The examination of four patients with division of both the median and ulnar (fig. 5) nerves supported the results found in the case of section of the individual trunks. In two there was an absolute loss of appreciation of passive movement

Fig. 5. Division of median and ulnar nerves.
■ = Complete loss of appreciation of passive movement.
▬ = Impaired recognition of passive movement.
Type *A* = 2 patients.
„ *B* = 1 patient.
„ *C* = 1 patient.

in all three joints of the little, ring and middle fingers and in the two interphalangeal joints of the index, whilst in the two joints of the thumb and the metacarpo-phalangeal joint of the index the perception was markedly diminished. The condition found in the other two patients only differed very slightly from the foregoing; in one the only difference was loss instead of defective perception at the interphalangeal joint of the thumb, and in the other loss instead of defective perception at the metacarpo-phalangeal joint of the index finger.

From the residual sensation it is easy to see that branches of the musculo-spiral contributed to the supply of the interphalangeal joint of the thumb in three out of the four, to the metacarpo-phalangeal joint of the thumb in all four and to the metacarpo-phalangeal joint of the index in three—results which are in precise agreement with the conditions found after division of the musculo-spiral.

MEDIAN AND RADIAL NERVES

An opportunity was offered of investigating one patient who suffered from division of both the radial and median nerves in the middle of the forearm. There was complete loss of appreciation of movement in both joints of the thumb and all three joints of the index and middle fingers; no disturbance could be detected in any of the joints of either the ring or little finger (fig. 6).

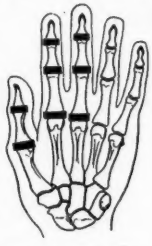

Fig. 6. Division of median and radial nerves.

COMMENTARY

From an analysis of the investigations recorded in this paper it appears possible to work out the regular source of supply of afferent fibres, conveying sensory impressions, to the joints of the fingers and thumb and also to establish the principal variations in distribution. The findings have been summarised in the table opposite. An attempt has been made to work out in percentages the occurrence of the commoner irregularities, but it ought to be stated that these figures can merely be considered as approximately accurate since only 51 patients were examined. The exact frequency of the various forms of distribution is not of any great practical service in clinical work; what appears to be more useful and of greater importance to the clinician, is to realise the intimate relationship between variations in the cutaneous and articular distributions of the various nerves. It is easy accurately to define and chart the former, and from this it is possible fairly accurately to forecast the distribution of that particular nerve to the joints. This relationship is of real value when endeavouring to estimate the extent of recovery in a patient who has not been examined previously, and whose form of distribution is not known unless previous clinical records are forthcoming. In the past too little attention has been directed to the examination of the power of appreciating passive movements

Thumb		Index			Medius			Ring			Little		
Inter-phal.	Met.-phal.	Distal Inter-phal.	Prox. Inter-phal.	Met.-phal.	Distal Inter-phal.	Prox. Inter-phal.	Met.-phal.	Distal Inter-phal.	Prox. Inter-phal.	Met.-phal.	Distal Inter-phal.	Prox. Inter-phal.	Met.-phal.
1. (Median chiefly Radial supplementary	1. (Radial chiefly Median supplementary	Median (invariably)	Median (invariably)	1. (Median chiefly Radial supplementary	Median (invariably)	Median (invariably)	1. (Median chiefly Radial supplementary	1. Ulnar (Probably supplemented by median)	1. Ulnar	1. Ulnar	Ulnar (invariably)	Ulnar (invariably)	Ulnar
2. Median alone 42 %	2. Radial alone 15 %			2. Median alone 25 %			2. Median alone 42 %	2. Ulnar alone 25 %	2. Ulnar alone 25 %	2. Ulnar alone 5 %			
	3. Median alone 16 %			3. Radial alone 8 %			3. Radial alone 8 %			3. Very rarely branches from radial			
				4. Very rarely some branches from ulnar			4. Rarely some branches from ulnar						

in patients suffering from injury to, or disease of, the peripheral nerves, and yet full information about this aspect of sensation is required in every case if the disability is to be assessed accurately and muscle training advised on a sound scientific basis for each individual patient.

It is not uncommon to discover, especially after suture of the median, that all the muscles—when tested individually—have recovered voluntary power, and yet the hand is of slight practical service when the patient attempts purposive movements. Further, it has been a frequent experience to hear patients complain, after an apparently successful suture of the median, that they find they lose the grip of their tools when they make an effort to work; and on further enquiry it is discovered that they can use the hand fairly well as long as they concentrate upon the movements, but it ceases to function satisfactorily as soon as they take their eye off it. Such patients also frequently inform you that the hand is useless in the dark, or when they cannot observe what they are trying to do with it. These complaints may be heard even when cutaneous sensibility has made a fair recovery and all the muscles, tested individually, exhibit a good range of voluntary movement. It seems clear that such disabilities are due to the loss of afferent stimuli from joints, muscles, tendons and other deep structures: but it is only really practicable to investigate directly the function of fibres conveying conscious impressions from such deep structures as joints. It was to obtain a knowledge of the normal distribution of these fibres, and the commoner variations, that the work described in this paper was originally undertaken. The application of these results, in the examination of the patients making the complaints just described, has shown that there is at the best a very defective recognition of passive movement in the joints supplied by the injured nerve, even when three years have elapsed since the time of the suture.

The further these investigations have progressed the more I have been impressed with the importance of an examination of the afferent nerve supply of the joints in all patients suffering from nerve injuries of the upper extremity, to be assessed for pensions; since the routine investigations of voluntary power and cutaneous sensibility do not, in themselves, provide sufficient information to determine the real functional capacity of the hand.

Previous reference has also been made to the significance of a knowledge of the power of appreciation of passive movement in all patients with disabilities of the hand to be treated by muscle re-education; the loss of this form of sensibility in peripheral nerve injuries offers a serious obstacle to the efficient application of this form of treatment—an obstacle which is probably insufficiently realised. Before the war our chief experience of muscle training was derived from the treatment of infantile paralysis, and consequently many who are responsible for the supervision of the administration of this form of treatment are content merely to develop an increased range of movement of the individual muscles, and fail to appreciate the very different problem which arises in peripheral nerve lesions. After injuries to the peripheral nerves there

is usually a serious loss of those afferent stimuli which are so necessary for the perfect performance and adjustment of the finer and more delicate movements, and consequently in the latter part of the treatment every effort must be made to develop those purposive and more complex movements which the particular patient will require when he returns to a suitable civil occupation.

To all who are familiar with the brilliant researches of Head upon the afferent system one result stated in this paper must appear astonishing. Head maintains that there is no loss of the sense of appreciation of movement in any joints when the median or ulnar nerves are divided at the level of the wrist, provided the nerve injury is not complicated by any division of tendons; since he holds the view that fibres subserving what he terms "deep sensibility" run mainly with the motor nerves and must pass to such deep structures as joints along the tendons and possibly the blood vessels. To uphold Head's contention with regard to deep sensibility the digital branches of the median and ulnar must be considered as cutaneous nerves, and yet a simple dissection of these nerves will clearly demonstrate branches passing to the periosteum of the phalanges and the interphalangeal articulations. It may be presumed that these branches of the digital nerves are either afferent or vaso-motor in function. The examinations recorded in this paper of patients suffering from division of the median or ulnar at the wrist and uncomplicated by any injury to the tendons, appear to show conclusively that some of these branches are afferent in function and transmit information which enables us to appreciate the site and direction of passive movement. As was pointed out at an earlier point in this paper, patients suffering from division of the median or ulnar nerve at the wrist are able frequently to recognise "movement" of a finger, probably as a result of alteration of tension or movement of the long tendons, but if care is taken it can be demonstrated easily that this knowledge is not produced by stimulation of afferent terminals in the neighbourhood of the joint.

My investigations fully support the view that some afferent fibres, distributed to subcutaneous structures, do pass probably along such channels as tendons, since a patient suffering from division of the median or ulnar is able to appreciate the application of pressure even on the digits. The significance and bearing of these results upon our conception of sensation must be dealt with fully in a subsequent paper.

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REPORT ON AN ANENCEPHALIC EMBRYO

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THE specimen which forms the subject of this report is a human embryo measuring some 17 mm., and presenting the condition of anencephaly. The stage of development, however, places the embryo among those of about 27 or 28 mm., and the details of its structure, apart from the abnormal regions, are quite comparable with those in a normal 28 mm., which I have consequently adopted as the standard by which the specimen is judged. I need not go into these particulars, and it will be enough, I think, to say that the specimen is one of anencephaly in a human embryo near the end of the second month; so far as I am aware, no record exists of a similar specimen of this age.

An outline reconstruction of the embryo is shown in fig. 1. It can be seen that, with the exception of the head, the general appearance of the embryo exhibits nothing unusual. It was divided into 10 μ serial sections, and these have been examined with a view to the discovery of any concomitant abnormalities.

(*a*) *Urinogenital System.* The anal end of the gut reaches the surface between the hinder extremities of the inner genital folds. The Müllerian ducts run down normally as far as the place where they cross over the Wolffian ducts, i.e. about the pelvic brim. Here, on the left side, the former duct apparently runs into the latter, while the right Müllerian duct disappears, though it cannot be definitely traced into the Wolffian duct. It may be remarked that examination of the genital glands suggests that the embryo is a male, whereas the 28 mm. "control" is female.

(*b*) *Alimentary and Respiratory Systems.* With the exception of the minor displacement of the terminal situation already noticed, nothing abnormal was found. The proximal limb of the U-loop was partly in the abdomen, and displaced above the distal limb and mesentery, but this was, I think, evidently accidental and referable to the preparation of the specimen: otherwise, the loop was normally in the umbilical sac.

(*c*) *Circulatory System.* Nothing abnormal found except in the head.

(*d*) *Skeletal System.* The cartilaginous skeleton appears normal, though there is a suggestion that the neural arches in the lumbar region, and perhaps elsewhere, are not quite as "thick" as in the 28 mm. sections. The impression of being thinner applies to all the tissues lying dorsal to the spinal cord, but there is absolutely no indication of any giving way or stretching to be observed.

(*e*) *Special senses.* The inner ear has reached a stage of development similar to that in the normal 28 mm. specimen, but the whole organ is rather smaller: the cells are probably smaller also, and, in the region of the proximal part of

the cochlear duct, they are destroyed or absent on the left side, possibly injured during sectioning. The tubo-tympanic region is normal.

The eyes are present, and present no evident abnormalities in the sections, but models show that the line of the choroidal fissure can be still appreciated, although the fissure itself is of course closed. It also seems likely that the formation of nerve-fibres is largely inhibited in these eyes, but no methods of special staining were used.

Fig. 1. Linear reconstruction of anencephalic embryo. The shaded areas in the head indicate certain nerve positions. *V*, *V*, the fifth nerve and its attached root; *IX*, *X*, *XII* are corresponding nerves. Some nerve remnants lie along the ventral surface of the elongated hind-brain stem. *Pit.*, marks the situation of the pituitary rudiment. *M.C.* is the upper end of Meckel's cartilage.

The nasal cavities are only apparently abnormal in their shape: this is projected on the drawing in fig. 1 by a dotted line, giving a somewhat triangular outline. The upper angle is prolonged into a small tube of epithelium, drawn out to reach the meningeal level of the skull-base. The anterior nares lead into the cavities through elongated canals. The palate folds lie above the tongue, not in contact with each other: it is probable, I think, that this position had been acquired after death.

Spinal cord. This appears to be quite normal, similar in size and structure

to that in the 28 mm. embryo, and extends to the tail region, as shown in the figure. The spinal nerves also call for no comment; the position of the first cervical nerve is indicated in the figure, and it may be said that in this case there was a tendency to separation of the nerve filaments from the cord.

Head and brain. The brain is represented (see figure 1) by an elongated portion of the hind-brain, ending fairly abruptly above, and by a pituitary body (*X* in the figure) and optic stalks and eyes. The pituitary body is smaller than in the 28 mm. specimen, but is almost as well developed, presenting a posterior lobe with the antero-lateral cornua growing up on each side of its stalk. There are cellular outgrowths from the lower part of the glandular portion, and the infundibulum is broken and ragged. The two pituitary organs are shown in fig. 2. The optic stalks begin in front of, and lateral to, the pituitary, from a small chaotic mass of *quondam* brain-tissue, and run outwards and downwards to the eyes: they are hollow for some distance.

All the cranial nerves are present in position below the base of the skull. Some of them are indicated in fig. 1, where the shaded projections give the positions of the trigeminal ganglion (*V*), ninth, tenth, and eleventh nerves. Traced proximally, all the nerves reach the meninges, where they come to an end, evidently torn: it may be pointed out here that the optic nerve does the same, and the olfactory fibres, quite apparent in their lower parts, are lost in the meningeal level with the upward tube-like prolongations of the nasal cavities. On comparison of the nerves with each other, there is found a marked difference between the third nerve and other nerves in the same sections of the orbit, the former nerve being little more than a vacuolated framework: this, for want of a better term, might conveniently be called degeneration. Muscles supplied by the nerve did not appear to be changed. No "degeneration" was found in the fourth nerve, and no change was apparent in the facial after giving off the chorda tympani—in fact no change could be certainly made out in any cranial nerve other than the third.

A space exists above and behind these broken ends of the cranial nerves on the meningeal aspect of the skull-base, and separates them from the remnant of the hind-brain. This space has evidently resulted from the straightening out of the hind-brain, which should, of course, occupy this region of the cranial cavity by its pontine flexure. The cavity presents occasionally in the sections a certain amount of débris, which in some cases is evidently nervous, and in others no doubt is meningeal.

The only part of the brain which remains—with the exception of the infundibular remnant and the basal débris—is the lower portion of the hind-brain. Reference to fig. 1 will show that the spinal cord is carried up to the head and becomes continuous there with an elongated column of nervous tissue which is directed upwards and forwards, ends somewhat abruptly above, and is surrounded dorso-laterally in its upper part by a broken mass of folded layers which are evidently remnants of the roof-plate of the rhombencephalon: a

well-formed choroid plexus[1] is recognisable as being made by the dorsal and upper part of these layers. The neural cavity begins to show a dorsal broadening shortly after passing into the skull, and, some little distance further up, opens out rapidly, so that this part of the brain-stem is widely open dorsally when it has extended up half the distance shown in the figure. The open "ventricle" is, of course, roofed by the layers already referred to, but the attachment of these to the stem is only occasionally visible, possibly owing to changes in this upper end during preparation.

The whole structure is related, on its ventral aspect at any rate, to membranes in which are vessels and remnants of nerves. These nerves cannot be traced into the stem, consist of groups of fibres and ganglionic masses, and may run through several slides. No indication is found, however, to point to the different nerves represented, and it may be said at once that none of the lower cranial nerves can be found attached to the stem. These remains of nerves are represented in the figure by a few shaded areas along the ventral side of the main stem, and among them is a large ganglionic mass lying above the trigeminal ganglion: it does not seem, however, to be a portion of that ganglion, and its real value, like that of the other remains, is doubtful.

When we come to the upper end of the main stem, however, there is, on each side, a large nervous attachment ventro-laterally, and this can be recognised (*V* in fig. 1) with certainty as the superficial origin of the fifth nerve. The recognition was made first from its size and general relations to the other parts, and was clinched by examination of its deep strands and relations within the stem.

It is only a short stump on each side, and has apparently been carried away from its ganglion by extension of the main stem. The stem comes to an end a little distance above the situation of this nerve stump.

Miss I. C. Mann made a reconstruction model for me of this piece of the brain-stem, which confirms the short account just given. The dorsal view of the model, however, is of sufficient interest, I think, to merit further investigation. It is shown, after removal of the folds of the roof plate, in fig. 2, with a drawing of the hind-brain of the 28 mm. embryo, seen from the left. Dealing first with the normal specimen, the dorsal portions of the spinal cord are seen to end in the dorsal tubercles *D* (paired), and in front of this the widely open rhombencephalic cavity is covered by the broad roof-plate, of which the attached edge only is shown. Within this cavity the dorsal lamina of the front limb of the pontine flexure (metencephalon) is thickening as a cerebellar plate (*Cbm*). Caudal to this, just behind the angle of the flexure, is a small but well defined area, *A*, in evident connection with the auditory nerve, while the paired prominences of the myelencephalic floor of the cavity lie caudal to these auditory areas. The positions of origin of the fifth, eighth, ninth and tenth nerves

[1] It is commonly stated that the choroid plexuses are formed in the fourth month. This is not correct: they begin to appear at or just after the middle of the second month, and grow steadily after this. When I speak of the plexus as "well-formed" in this specimen, I am of course referring to its proper stage of development.

are also shown. Turning now to the abnormal brain, the dorsal tubercles are recognised at once at *D*, and the open region above these is the rhombencephalic cavity, the floor of which is exposed as a result of removal of the roof-plate. But the rounded and prominent masses seen in this floor, *V*, are not metencephalic, such as would be their value if seen from a dorsal view of such a brain as that of the 28 mm. specimen: they are the floor masses of the myelencephalon, brought up above the level of the dorsal tubercles as a result of the straightening out of the flexure. Thus, cranial and lateral to them, we recognise the auditory area *A*, from which a groove extends upwards and inwards and probably marks the line of the flexure.

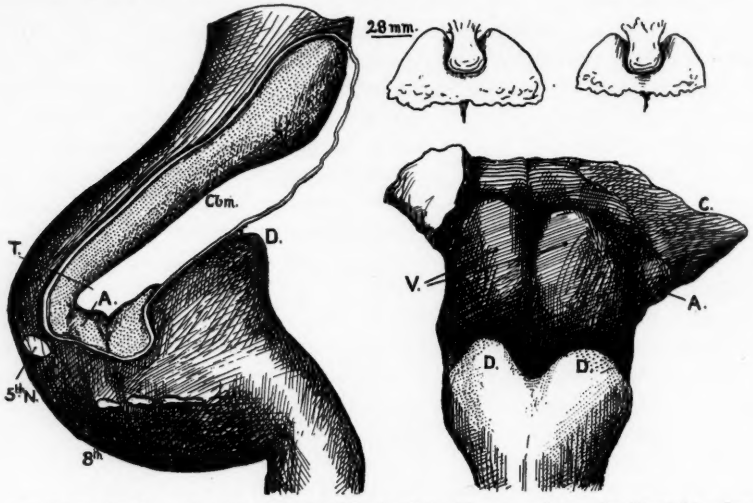

Fig. 2. On the left is a side view of the hind-brain of the 28 mm. embryo. On the right a dorsal view of the brain stump in the anencephalic specimen. The small figures above this are from reconstructions of the pituitary bodies in these two embryos. *A*, the auditory area; *C*, the everted cerebellar plate; *Cbm*, the same plate in normal position; *D*, the dorsal tubercles in both brains; *V*, the ventral laminae of the myelencephalon; and *T*, the approximate level of destruction.

Further up and further out, the dorsal lamina or cerebellar ridge (*C*) is present in part on one side, while it is folded in on the other side. This reading of the condition present is in accord with the previous description of the origin of the fifth nerve, which is now seen to bear exactly similar relations to the various parts of the hind-brain in the two specimens. We thus reach the conclusion that the brain-stem of the anencephalic embryo comes to an end at a level which might be represented on the normal 28 mm. reconstruction by the line *T*, drawn through the lower part of the metencephalon.

Inferences to be drawn from the conditions in this embryo which have been described are that there has been a secondary separation of the cranial nerves from their attachments to the brain, and that the remnant of the brain, free

from controlling forces holding it down in position, is no longer bent but has straightened itself and grown up in a direct line with the cord. I do not think there can be reasonable doubt that a brain existed: the presence of eyes, of a neural pituitary outgrowth, of third and fourth nerves, and incidentally of the nervous débris found in the cranium, indicate this very clearly. If, then, we start with the conception of a brain being present, it follows that this must have undergone destruction at a later period, and I think that this catastrophe might reasonably be referred to primary and secondary causes. We must, I think, assume the previous presence of the brain, but we cannot and ought not assume that this brain was normal. The present specimen gives no hint about the nature of that fundamental abnormality, but no doubt the tendency would be to place it in the dorsal laminae or roof-plate, or, taking what is only an intercurrent effect, to assume the existence of an embryonic hydrocephalic condition. As just said, the specimen does not appear to give any clue to this, and it remains open to anyone to maintain his own views as to this primary fault. The ventral laminae were evidently able to form third and fourth nerves: further than that it does not seem possible to go in drawing inferences as to their condition, except that they appear perfectly good, so far as they exist, in the stump of the hind-brain.

But whatever the nature of the primary fault, it is clear that it must result in destruction of the continuity of the brain-stem at some point or points. In the present specimen I have the impression—to which I will refer again—that this destruction of the continuity of the tube occurred in the fore-brain, about the region of the rudiments of the corpora mammillaria: it is easy to formulate theories connecting this situation with deficiencies in dorsal and cerebral development. With this necessary solution of the tube, it seems to me that the action of the primary cause may be considered to have reached its acme and now, by virtue of this primary result, the secondary causes come into play and complete the destruction of that part of the brain affected by them.

Some years ago (*Lancet*, 1916) I described the pituitary region of the brain as the most "fixed" place within the skull, and referred the formation of the mid-brain flexure to the forward growth of the hind-brain acting against this fixed point. I have no wish to put forward any far-reaching morphological argument on this point, which I simply advance for what has always seemed to me to be its mechanical value: the definite adhesion of stomodaeal and neural ectoderm at this place, and their association with the upper end of the buccopharyngeal membrane, Seessels' pocket (when present), and the adherent notochord, seem to me to give a guarantee of fixation, supported by every sagittal section, which must influence the shape of a brain growing up against its fixation here. The brain, growing more rapidly than the skull-base, piles itself up into curves, so to speak, and these then owe their existence, mechanically, and at least in part, to this fixation of the fore-brain. So, if the continuity of the brain is destroyed behind this fixed region, there is not the mechanical fixation or point of resistance against which the growing brain can produce or

maintain curves, and the result is that there is a tendency for the stem to become straight behind the site of the destruction. This is seen in the straight stump left in this specimen, and would reasonably be certainly expected to occur in the mid-brain curve, if the destruction takes place anterior to this. But the straightening out of these curves involves rupture of all structures which pass between them and fixed points in their neighbourhood, and thus we come to secondary rupture of nerves and vessels.

So far as concerns the nerves, there are at least two possible explanations of the nerves being found broken off short at the meningeal level—they may have been ruptured by the straightening out of the curves, or they have been left free as a result of destruction of their sites of origin, without being previously separated from the stem. In this connection it is interesting to consider the hind-brain. Here we find the great fifth nerve evidently torn and yet with its torn root still in position in the brain, and the lower nerves, also torn, have certainly suffered this fate before the destruction of the brain-stem. Hence we can conclude that the rupture of nerves as a result of straightening of the brain can certainly take place, and is probably easier to accomplish than we perhaps imagine, influenced no doubt largely by our experience of adult nerves. This is suggestive, but of course not conclusive, for the third and fourth nerves: we can leave the matter there for the moment, and turn now to the vessels.

The internal carotids are large vessels, of normal appearance and running a normal course up to the origin of the ophthalmic arteries. These branches are of normal size, and the carotids go on after their origin for a little distance, and then abruptly come to an end, with open mouths. It is evident that they have been torn across, and it would seem that this is a result of the same processes which have torn the nerves. The vertebral arteries, lying in the meningeal tissues on the ventral side of the hinder stump of the brain, join here to form a basilar artery, and this is drawn out on the ventral surface of the stump, practically to its upper end: probably this is the end of the artery, but its division could not be absolutely demonstrated, as the membranes get very ragged at the upper end. This system is composed of vessels of good size, giving off good-sized branches. If we can judge from the remains of the carotid and vertebral systems, there was nothing wrong with these to account for the primary failure in development, but they have been secondarily affected as a result of the primary failure.

The position of the rupture of the carotids seems to me to suggest that the solution of continuity of the brain-stem took place not very far away—in fact, it was an important factor in forming my opinion that this destructive lesion occurred just above the infundibular outgrowth, the other considerations having mainly to do with the structure of this part and its connections with cerebral and other dorsal derivatives. A rupture in this place fits in well with the conditions that were found, want of fixation of the brain-tube behind the situation leading to rupture of nerves, and failure of blood supply leading to

disappearance of tissue. In accordance with this is the fact that the pituitary and eyes, whose vascular supplies remain, are still present, while the cerebral system supplied by the carotids above this level has utterly disappeared: also the hind-brain remains as far as the vascular supply is present and then ends abruptly, although there is nothing in the structure, examined microscopically, to distinguish this from any other hind-brain of the same stage and at the same level.

A reconstruction of the skull-base showed that it was comparable in development with the 28 mm. skull in its post-pituitary portion, except that the otic capsules showed a tendency, perhaps, to stand up more from the level of the floor, suggesting that there had not been any hind-brain structures lying on this floor for some little time: but, in front of the infundibular region, the base was narrowed and shortened, giving the impression of belonging to an earlier stage, although its cartilaginous and other details were in keeping with those of the "control." The eyes projected out for a considerable distance beyond the side levels of the front part of the skull. The frontal wall of the cranium was folded back sharply over the front of the base, and turned down here, ending in a thinned edge; there were no indications of the occipital sinking so noticeable in older anencephalics.

To sum up, this specimen appears to me to suggest that, although the original and primary cause of anencephaly may be some local defect, limited perhaps to the fore-brain region, or may be of different nature in different cases, secondary causes of the condition ultimately found may also occur: that these secondary conditions result from rupture of the brain-stem and consequent loss of fixation of the front end of this growing stem: that as a result of this the curves tend to straighten out: that consequently the nerves and vessels connected with it give way: and that the brain tissue, as a result of the vascular starvation, breaks up and disappears up to the limits of the remaining blood supply. The specimen does not appear to offer any explanation of the nature of the primary fault.

THE SKULL AND SOME RELATED STRUCTURES OF A LATE EMBRYO OF LYGOSOMA

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The skull described in this paper is that of an embryo *Lygosoma* of unknown species belonging to the collection of Prof. J. P. Hill. The accompanying text-figures are of a wax plate model constructed from drawings of the transversely-sectioned head of the embryo, the actual length of which was about 4·8 mm. The model represents a magnification of approximately 100 in the transverse plane but only of about 75 in length, and this telescoping is of course reproduced in the drawings. The left half of the brain was included as a support.

The model was made at the suggestion and under the direction of Mr D. M. S. Watson, who helped in the construction of it and has throughout given advice, criticism and assistance. It was intended to serve as a basis of comparison for fossil skulls, certain blood-vessels, nerves and muscles being included in order to demonstrate more clearly the relations of the hard parts: it may be analogised with the standard solution of the chemist.

OTIC REGION

This region of the cranium is very largely ossified, the various bony elements having nearly attained their adult relationships, though still separated from each other by larger or smaller strips and blocks of cartilage into which no bone has yet extended. One such strip runs right along the ventral surface of the ear capsule, separating the basisphenoid and basioccipital below from the pro-otic, opisthotic and exoccipital above. The pro-otic, opisthotic and supra-occipital are also separated from each other by cartilaginous areas. Between the exoccipital and opisthotic alone no cartilage remains and the suture is difficult to determine, but the foramen for the tenth nerve, which passes out of the cranium immediately behind the ear capsule, appears to lie between the two bones.

Anteriorly the processus anterior inferior (figs. 1 and 2, *P.A.I.*) of the pro-otic extends forwards in front of the ear capsule beneath the big pro-otic notch for the fifth nerve as a thin sheet of bone leaning outwards from the brain below the gasserian ganglion, its upper edge rolled over scrollwise where it affords attachment for the protractor pterygoid muscle. This process, like the ventral edge of the rest of the pro-otic, is still continuous with the strip of cartilage mentioned above as forming the lateral boundary of the basisphenoid; ossification is extending downwards into the cartilage from the pro-otic and upwards into it from the basisphenoid. The process ends at about the level of the back wall of the pituitary fossa.

On the inner side of the ear capsule the pro-otic extends back to the foramen acusticum posterius which it almost, but not quite, surrounds, the postero-ventral boundary of the foramen being still cartilaginous. Behind this foramen the supraoccipital extends nearly half way down the inner wall of the capsule, enclosing the foramen endolymphaticum, while the ventral half is now formed by the opisthotic. This is the region of the sinus superior utriculi of the membranous labyrinth.

On the outer side of the ear capsule the pro-otic extends back above the fenestra vestibuli to the region where the supra-temporal pushes in between the upper end of the quadrate and the prominence for the external horizontal canal. This is just anterior to the paroccipital process (crista parotica of Gaupp[1]) which is itself still cartilaginous.

The anterior extremity of the opisthotic on the outer side of the ear capsule is below and just anterior to the fenestra vestibuli and paroccipital process.

The supraoccipital extends forwards to a point above the foramen acusticum posterius. It completely surrounds the posterior extremity of the anterior vertical semicircular canal and reaches down on the inner surface of the ear capsule to enclose the foramen endolymphaticum (as described above), while on the outer surface of the capsule it extends half way across the dorso-lateral wall till it meets the cartilaginous region surrounding the external semicircular canal and continuous with the paroccipital process. It completely surrounds the anterior extremity of the posterior semicircular canal and in this region arches over the cranial cavity, the tectum synoticum being ossified except for a cartilaginous core continuous in front with the anteriorly projecting processus ascendens. Behind the tectum, in the region where the posterior semicircular canal is passing outwards and downwards, the supraoccipital is rapidly excluded from the wall of the canal, the bone narrowing to its posterior extremity which is just above Gaupp's orificium posterius of the external semicircular canal.

In the floor of the brain case the basioccipital runs forwards as a very thin plate of bone bounded at the sides by the thick cartilaginous strip which separates it from the exoccipital and otic bones. Posteriorly it broadens out into the cancellous condylar portion, sheathed in cartilage. Anteriorly, just in front of the anterior end of the cochlear canal, it thins out in the membrane which separates it from the basisphenoid. This membrane closes the reduced basicranial fenestra (fig. 1, ***B.F.***), the thin bony plates bounding it in front and behind probably having been formed by extension into an originally much larger membranous area such as is present in Gaupp's 31 mm. *Lacerta* and stage 5 of Rice's[2] *Eumeces*.

There is no trace of the notochord within the cranial region.

The thin plate of basisphenoid in front of the fenestra does not extend back quite to the level of the posterior edge of the pro-otic notch. Passing forwards

[1] Gaupp, 1900, *Anatomische Hefte*, Bd. xv, Heft 3.
[2] Rice, 1920, *Journal of Morphology*, vol. xxxiv.

beneath the fore-brain it rapidly thickens dorso-ventrally and narrows from side to side, forming a cancellous bony plate below the notch, but still separated from the pro-otic by a strip of unossified cartilage which continues forwards in front of the processus anterior inferior of that bone along the edge of the plate to its anterior extremity.

At either edge of the ventral surface of this plate the palatine branch of VII and the internal carotid artery (fig. 1, VII, P^1 & *I.C.A.*) lie in a groove which runs anteriorly for a short distance and then plunges into the substance of the bone to form the Vidian foramen. The place of exit of the latter is on the

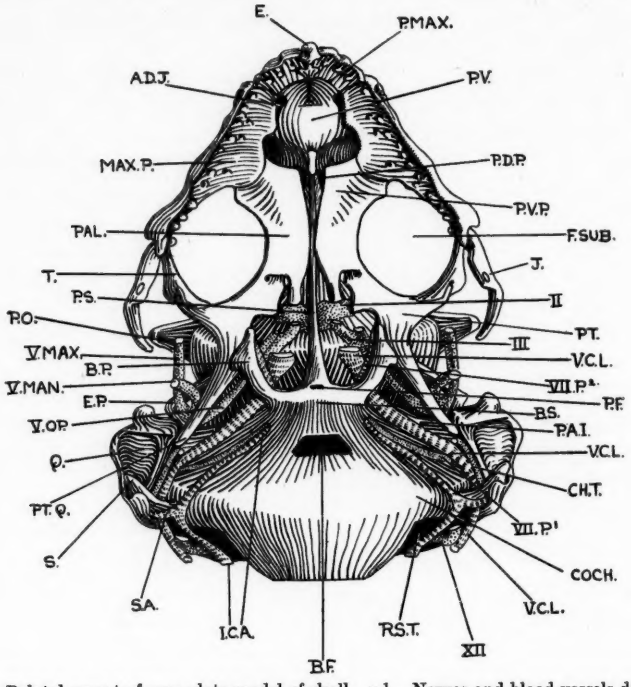

Fig. 1. Palatal aspect of wax plate model of skull. ×¾. Nerves and blood-vessels dotted. Jaw, hyoid and muscles removed. (Brain included in model for support.)

anterior edge of the plate just mesial to the root of the basipterygoid process (fig. 1, VII, P^2 & fig. 3, *V.F.*).

Anteriorly the plate is scooped out between the two Vidian foramina to form the pituitary fossa, in which the proximal ends of the posterior rectal eye muscles, attached to the floor of the fossa, may be seen lying on either side of the hypophysis cerebri.

Immediately after entering the Vidian foramen the internal carotid artery branches, one small branch running forwards with the palatine of VII in the

foramen, while the main branch passes into the pituitary fossa and upwards through that to the ventral surface of the brain.

The N. abducens, running forwards below the brain, enters the basisphenoid from above, just behind the place where the palatine of VII and the internal carotid artery enter it from below. It runs forwards in the bone for a short distance and enters the pituitary fossa lateral to the internal carotid artery as that vessel passes up to the brain. The nerve at once comes into contact with the proximal end of the posterior rectus and seems to enter that muscle before it passes out of the pituitary fossa.

On either side of the pituitary fossa the basisphenoid still retains its thick cancellous nature but over the floor of the fossa it consists of a very thin bony plate. Towards the anterior end of the hypophysis the fossa shallows out, the thicker lateral portions of the basisphenoid approach each other in the mid-line, and the anterior extremity of the thin floor between them is perforated by the very small membrane-closed pituitary foramen (fig. 1, *P.F.*).

SUMMARY OF NERVE EXITS

V. The trigeminal, after a short forward course within the cranium, passes out through the pro-otic notch. The big gasserian ganglion (fig. 2, *G.G.*) is sheltered dorsally by the anterior end of the ear capsule, postero-ventrally by the outwardly bent processus anterior inferior of the pro-otic (fig. 2, *P.A.I.*), so that it lies almost intra-cranially. From the ganglion the three main branches of the nerve run forwards, the ramus ophthalmicus (figs. 1 and 2, V, *OP.*) inwards mesial to the epipterygoid, the rami mandibularis (V, *MAN.*) and maxillaris (V, *MAX.*) outwards laterally to that bone.

VII. The facial nerve arises by the same root as V but passes straight out of the cranium so that its foramen lies at a short distance posterior to the pro-otic notch and slightly more ventral. The foramen is very small, piercing the pro-otic immediately under its capsular portion. The geniculate ganglion lies just in front of the foramen, and from it the ramus palatinus (fig. 1, VII, *P.*) passes downwards and forwards close to the cranial wall, the ramus hyomandibularis backwards along the outer surface of the ear capsule.

VIII. The root of the auditory nerve lies immediately posterior to and above that of VII. The foramen acusticum anterius for the vestibular branch perforates the pro-otic above the anterior end of the cochlear canal. The foramen acusticum posterius for the cochlear branch lies at the extreme postero-median limit of the pro-otic, part of the posterior and ventral boundaries of the foramen being still cartilaginous.

IX. The glossopharyngeal does not pass out of the cranium through the foramen which leads into the recessus scala tympani (figs. 1–4, *R.S.T.*) as in *Lacerta* (Gaupp), *Varanus bivittatus* (Watkinson[1]), and some of the stages of *Eumeces* observed by Rice, but has a separate small foramen immediately above and in front of this and also leading into the recessus. Possibly, earlier

[1] Watkinson, *Morphologisches Jahrbuch* Bd. xxxv.

in development, the two were confluent as in *Lacerta*, their separation being due to the extension of the cranial wall in this region—a continuation of the process of extension which earlier still divides the originally single metotic fissure into a posterior "foramen jugulare" and an anterior perilymphatic foramen.

These foramina pierce the opisthotic at its antero-ventral extremity, just posterior to the pars cochlearis of the ear capsule (figs. 1–4, *COCH.*).

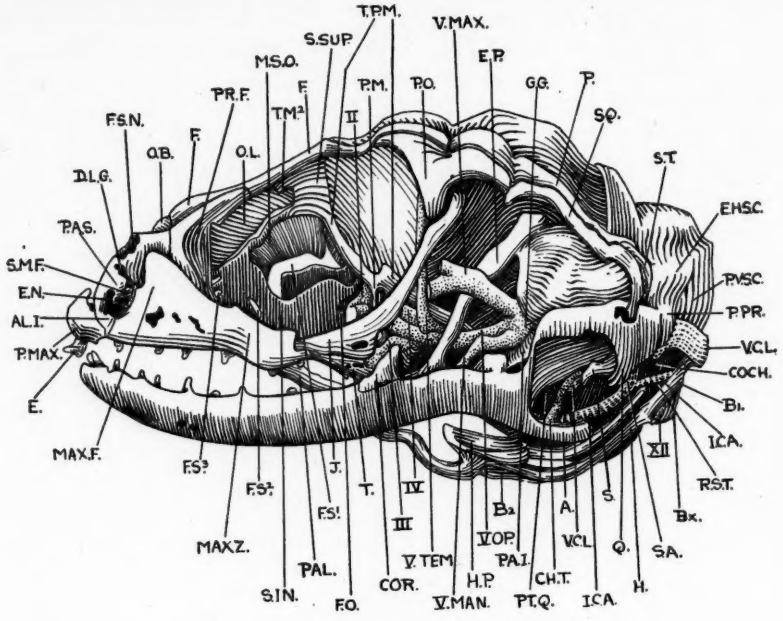

Fig. 2. Left lateral view of same model. ×$\frac{1}{4}$.

The glossopharyngeus runs back along the dorso-medial border of the recessus scala tympani to pierce the membranous wall of the latter at its posterior extremity. Outside the recessus it comes into contact with the hypoglossus and vagus, at the point where these two cross each other, and is joined by a branch of the hyomandibular of VII.

X and XII. The several small roots of the vagus join to form one large nerve which leaves the cranium at the back of the ear capsule between the opisthotic and exoccipital. Ventral to this the exoccipital is pierced by two foramina for the roots of the hypoglossal, one immediately in front of the vagal foramen and beneath the posterior end of the ear capsule, the other a little behind it.

The anterior root of XII runs straight out laterally under the ear capsule; the posterior root, after being joined by a branch of the first spinal, runs

forwards to meet the anterior root. At the point where these roots unite the hypoglossal turns forwards and is crossed by X which loops back beneath it.

RECESSUS SCALA TYMPANI AND RELATED FORAMINA

The conditions in that region of the ear where the perilymphatic duct—of which the scala tympani is phylogenetically a modified portion—passes from it and into the cranium cannot be homologised directly in lizards and mammals, but must be referred to a common Cotylosaurian ancestor. The mammals appear

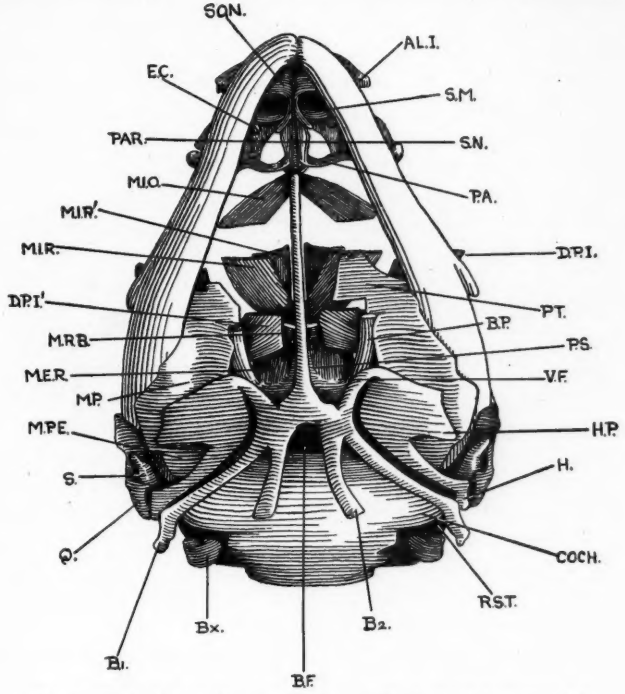

Fig. 3. Ventral view of same model. ×¼. Most of palate removed to show muscles. Nerves and brain omitted.

not only to have evolved further in this respect but also along a rather different line. Therefore it is difficult to apply the mammalian nomenclature of fenestra cochleae or rotunda, and aqueductus cochleae, to the structures present in a lizard. Neither, however, will the nomenclature used by Gaupp for *Lacerta* and, with modifications, by Rice for *Eumeces*, fit in with the very definite arrangement found in *Lygosoma*, the stage here described being evidently later in development.

In this lizard the recessus scala tympani (figs. 1–4, *R.S.T.*) is a well defined chamber lying beneath the ear capsule immediately behind the cochlear

prominence (*COCH.*). The perilymphatic duct enters this chamber by a foramen in its roof and swells out into a big saccus perilymphaticus; from this, perilymphatic tissue passes into the cranial cavity through a foramen in the mesial wall of the chamber just below the one in its roof. In front of these two foramina, which lie in the same transverse plane as the paroccipital process and thus well in front of the foramen for the Xth nerve, the back of the cochlea prominence projects down to form the anterior wall of the chamber; behind them the latter stretches back for some distance. The concave ventro-lateral wall of the chamber is formed throughout by a very definite, clearly-defined membrane, which stretches from just above the cartilaginous strip of basal plate separating opisthotic from basioccipital upwards and outwards to the ventro-lateral edge of the ear capsule. This membrane also arches up behind to form the back wall of the chamber.

Gaupp's name of "medial aperture of recessus scala tympani" may be applied to the foramen through which the perilymphatic duct enters the cranium, but the whole of the extensive ventro-lateral and posterior walls of the recessus can hardly be referred to as its lateral aperture, in spite of its being composed of membrane only.

ORBITO-TEMPORAL REGION

At the level of the small pituitary foramen (fig. 1, *P.F.*) the basisphenoidal plate (fig. 1, *B.S.*) ends abruptly, passing over into the presphenoidal cartilage (figs. 1 and 3, *P.S.*) in the mid-line, and the basipterygoid processes (figs. 1 and 3, *B.P.*) laterally. The origin of the presphenoidal bar from paired trabecular cartilages is evident at its root, which is a double structure, the two halves (corresponding to the longer "trabeculae" of *Lacerta*) being continuous with the just ossifying block of cartilage on either side of the pituitary foramen.

This presphenoidal cartilage runs right forwards through the orbital region and is continued into the base of the septum nasi (figs. 3, 4 and 6, *S.N.*). It lies well above the bony palate and is itself simply the ventral edge of the neural cranium in the orbito-temporal region—a region which is here, as in all lizards, much fenestrated, and compressed between the eyes into a narrow interorbital septum in correlation with the enormous size of these organs. The reduction of the chondrocranium in this region has proceeded even further than in the stage modelled by Gaupp (1900) and is perhaps intermediate between the conditions in stage 2 and stage 5 of *Eumeces* figured diagrammatically by Rice (1920) but does not quite correspond to either.

Of the cartilaginous bars in the temporal region resulting from this fenestration, the following, after Gaupp's nomenclature, are present in part or whole.

1. *Taenia marginalis.* This is only represented at its extreme posterior (fig. 4, *T.M.*[1]) and anterior (fig. 2, *T.M.*[2]) ends. Posteriorly as a slender rod of cartilage arising from the dorsal surface of the ear capsule in the cartilaginous region which separates the supraoccipital and pro-otic ossifications, and projecting forwards for a short distance above and parallel to the ridge for the anterior vertical semicircular canal (fig. 4, *A.V.S.C.*). Anteriorly as a

similar but even shorter projection from the antero-dorsal edge of the solum supraseptale (figs. 2 and 4, ***S.SUP.***) (just as in Gaupp's model) and under cover of the lateral edge of the frontal (fig. 2, ***F.***).

2. *Taenia parietalis media* (figs. 2 and 4, ***T.P.M.***). This is present throughout its whole length, forming the dorsal margin of the fenestrae optica (fig. 2, ***F.O.***) and metoptica, and lying close against the antero-ventral wall of the fore-brain, between that and the posterior eye-muscles.

3. *Pila pro-otica* (fig. 4, ***P.P.***). This is simply represented by the blindly ending posterior extremity of the taenia parietalis media, bent round at right

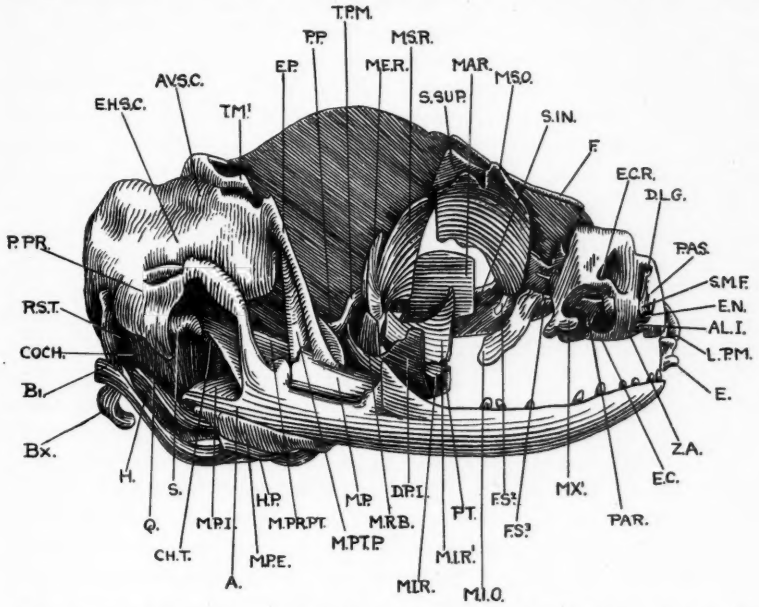

Fig. 4. Right lateral aspect of same model. ×¼. (The left half of the brain is included in the model for support.)

angles to the rest of the latter so as to point caudally, and quite failing to reach the basis cranii. From its ventro-median border originates the depressor palpebrae inferioris muscle, which passes forwards and divides into two, a small group of fibres (fig. 3, ***D.P.I.***[1]) passing inwards to the soft palate and a broad thin sheet (figs. 3 and 4, ***D.P.I.***) passing forwards and outwards under the eye to be inserted in the lower eyelid and on the posterior edge of the membrane covering the suborbital fenestra (fig. 1, ***F.SUB.***).

4. *Pila metoptica* (fig. 2, ***P.M.***). This is complete, lying close against the antero-ventral surface of the fore-brain, at right angles to the taenia parietalis media and the presphenoidal cartilage, and forming the posterior margin of the fenestra optica.

The pila of either side meets its fellow below the optic chiasma and the single bar thus formed bends straight down away from the brain to join the presphenoidal cartilage. The superior recti muscles take origin from either side of the place of union of the two pilae, while the inferior recti arise immediately in front of them from the posterior edge of the joint bar. The retractor bulbi muscles arise from the dorsal surface of the presphenoidal cartilage posterior to the region where this bar joins it.

The pila accessoria is entirely lacking.

Of the fenestrae of which these cartilaginous remnants form the boundaries, the fenestra optica (fig. 2, *F.O.*) is complete and transmits the optic nerve (figs. 1 and 2, II) only. The fenestra metoptica is confluent with the "fenestra" pro-otica at its postero-ventral corner owing to the pila pro-otica being incomplete. Gaupp's fenestra epioptica is entirely lacking, owing to the absence of a taenia marginalis in this region and of a pila accessoria. The "fenestra" pro-otica itself has no dorsal boundary, also owing to the absence of a taenia marginalis above the greater part of it.

The pro-otic space transmits the trigeminal nerve, the big gasserian ganglion (fig. 2, *G.G.*) lying in the usual notch in the pro-otic (incisura pro-otica of Gaupp). From the ganglion the maxillary (figs. 1 and 2, V, *MAX.*) and mandibular (figs. 1 and 2, V, *MAN.*) branches of the nerve pass outwards, laterally to the epipterygoid (figs. 1 and 2, *E.P.*), while the ophthalmic (figs. 1 and 2, V, *O.P.*) branch runs more medially, keeping near to the ventro-lateral surface of the brain, between that and the pterygoid muscles (fig. 4, *M.PR.PT.* and *M.PT.P.*) and above the edge of the basisphenoid; it runs along the ventral surface of the pila pro-otica (fig. 4, *P.P.*) and anteriorly to this gives off a small branch (ramus temporalis) (fig. 2, V, *TEM.*) which passes forwards with the main one for a short distance and then bends abruptly upwards along the lateral surface of the brain, crossing over the taenia parietalis media (figs. 2 and 4, *T.P.M.*). The main maxillary branch still runs forwards, keeping near to the ventro-lateral surface of the brain and coming into contact with the oculomotor (figs. 1 and 2, III), with which it runs parallel between the brain and the eye-muscles as far as the pila metoptica (fig. 2, *P.M.*).

From its origin on the dorsal wall of the mid-brain the trochlear nerve (fig. 2, IV) runs forwards and slightly downwards, and keeping very close against the brain wall it comes into contact with the taenia parietalis media (fig. 2, *T.P.M.*), lying at first dorsal to the latter and then ventral, and crossing it on its medial surface. In this part of its course it runs above and within the oculomotor and the maxillary ramus of V. Together with these it passes laterally to the pila metoptica (fig. 2, *P.M.*).

Thus, as in *Lacerta* and *Eumeces*, the three branches of the trigeminal pass out of the cranium through the fenestra pro-otica (incomplete dorsally), the trochlear and oculomotor through the fenestra metoptica, and the optic nerve through the fenestra optica.

ORBITAL REGION PROPER

The anterior part of the ethmoidal cartilage is represented solely by the fenestrated septum (figs. 2 and 4, *S.IN.*) between the eyes and a small dorsal portion, (solum supraseptale of Gaupp), (figs. 2 and 4, *S.SUP.*) still clasping the posterior end of the elongated olfactory lobes (fig. 2, *O.L.*). The ventral edge of the septum is confluent with the anterior end of the presphenoidal cartilage (fig. 1, *P.S.*). The septum is perforated by three membrane-closed fenestrae, a very large postero-dorsal (figs. 2 and 5, *F.S.*[1]) and two smaller antero-ventral (figs. 2 and 5, *F.S.*[2] & *F.S.*[3]). The lower half of its posterior border is curved forwards, forming the anterior edge of the fenestrae opticae (fig. 2, *F.O.*) while the upper half is a simple bar, triangular in section, supporting the antero-ventral surface of the fore-brain and bounding the large septal fenestra behind. This bar is directly continuous with the anterior ends of the taeniae parietales mediae (fig. 2, *T.P.M.*) which indeed seem not to fuse completely on joining it, as the bar appears double in section. Antero-dorsally, above the large septal fenestra, each half of the bar expands into a flat wing which runs up to meet the lateral edge of the frontal bone (fig. 2, *F.*) of that side, the short trough-shaped tunnel (figs. 2 and 4, *S.SUP.*) thus formed surrounding the olfactory lobes (fig. 2, *O.L.*) at their posterior end. The cartilaginous part of the tunnel is the solum supraseptale of Gaupp.

The taeniae marginales (fig. 2, *T.M.*[2]) constitute in this region a dorsal extension of the side wall of the tunnel. The ventral edge of the trough is continued forwards and slightly downwards as a narrow bar below the anterior end of the olfactory lobes; this joins the anterior part of the septum in front of the big septal fenestra, of which it forms the dorsal boundary.

In the region where the taenia parietalis media of either side joins the posterior edge of the septum, above the place where the two optic nerves separate from one another, is the more dorsal of the two origins of the internal rectus eye-muscle (figs. 3 and 4, *M.A.R.*), which runs anteriorly in a vertical plane between the septum and the back of the eye. The ventral origin of this muscle is on the dorsal surface of the presphenoidal cartilage below the optic fenestra. The two parts join each other immediately in front of the place of separation of the optic nerves.

The more posterior of the two small septal fenestrae (figs. 2 and 4, *F.S.*[2]) lies immediately in front of and below the large fenestra (*F.S.*[1]). On the anterior part of its closing membrane the superior oblique eye-muscle (figs. 2 and 4, *M.S.O.*) has origin. The more anterior of the two fenestrae (*F.S.*[3]) lies just behind the planum antorbitale (figs. 3, 6 and 7, *P.A.*) where the much narrowed interorbital septum (figs. 6 and 7, *S.IN.*) passes into internasal septum (*S.N.*); the closing membrane of this fenestra gives origin to the inferior oblique eye-muscle (figs. 3 and 4, *M.I.O.*). In Gaupp's *Lacerta* embryo there is only one fenestra in this anterior region of the septum. Rice finds that in *Eumeces* the extent of fenestration depends on the age of the embryo and the degree of resorption of the cartilage.

SUMMARY OF EYE-MUSCLES

Fig. 5 is a diagrammatic representation of the orbito-temporal region of the cranium in which the places of origin of these muscles are indicated by cross-hatching.

1. *External Rectus* (figs. 3 and 4, *M.E.R.*). Origin: on floor of pituitary fossa at side of hypophysis and forwards along dorsal surface of presphenoidal cartilage until replaced by fibres of retractor bulbi. Muscle passes forwards close to brain and then spreads out in front of the taenia parietalis media (fig. 4, *T.P.M.*) into a flat sheet at back of eye. Before doing this it gives off a large clump of fibres, a few of which pass up to join the superior

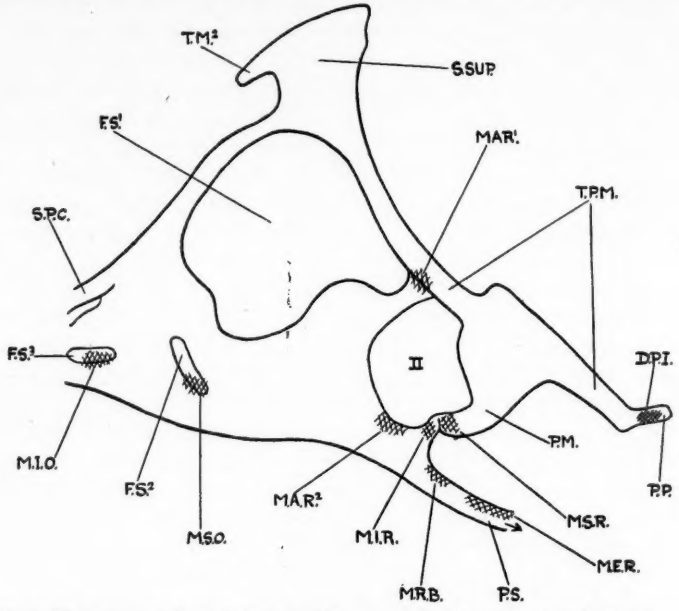

Fig. 5. Diagrammatic lateral view of orbito-temporal region of cranium to show eye-muscle insertions (cross-hatched). $\times \frac{1}{2}$.

rectus, the remainder passing forwards and downwards to form an accessory inferior rectus (figs. 3 and 4, *M.I.R.*[1]) lying closely within and above the other one but never fusing with it.

2. *Superior Rectus* (fig. 4, *M.S.R.*). Origin: on pila metoptica at the place where it meets its fellow beneath the brain at back of optic chiasma. Muscle runs forwards and upwards at side of latter against anterior surfaces of pila metoptica and taenia parietalis media, and is joined beneath its insertion by a few fibres from the external rectus.

3. *Inferior Rectus* (figs. 3 and 4, *M.I.R.*). Origin: just in front of superior rectus on short bar formed by union of pilae metopticae above and joining them

to presphenoidal cartilage. Muscle passes forwards and outwards in a horizontal plane just below edge of septum.

4. *Internal Rectus* (figs. 4 and 5, *M.A.R.*). Origin: (*a*) by fibres arising from place where taenia parietalis media joins the cartilage bounding the big fenestra septi behind and representing posterior edge of septum; (*b*) by fibres on dorsal surface of presphenoidal cartilage below optic fenestra. The two groups join together in front of optic nerve, the main body of the muscle running straight forwards between eye and septum.

5. *Retractor Bulbi* (figs. 3 and 4, *M.R.B.*). Origin: partly on dorsal surface of presphenoidal cartilage anterior to the fibres of external rectus, but mainly further forwards on this cartilage below the origin of inferior rectus described above. Muscle is a slender one running straight out to side to be inserted on eye just below and in front of insertion of posterior rectus.

6. *Superior Oblique* (figs. 2 and 4, *M.S.O.*). Origin: on anterior part of membrane closing hindermost of the two small septal fenestrae (*F.S.*^{2}). Muscle passes upwards and backwards along surface of septum and of membrane closing big posterior septal fenestra, being inserted on eye in region of solum supraseptale.

7. *Inferior Oblique* (figs. 3 and 4, *M.I.O.*). Origin: on closing membrane of foremost of the two small septal fenestrae (*F.S.*^{3}).

OLFACTORY REGION

Incomplete as are the walls of the nasal capsule, the olfactory organs are well protected on all sides owing to the development of membrane bones over those regions where cartilage is lacking. In general plan the capsule itself agrees fairly closely with that of *Lacerta*, the differences being principally a matter of proportion and degree of fenestration. The large fenestra lateralis nasi described and figured by Gaupp in the wall of the extraconchal recess is, as in *Eumeces*, entirely lacking, while, also in agreement with stage 5 of *Eumeces*, the small fenestra superior nasi of Gaupp is so large that it occupies about half of the antero-dorsal slope of the nasal capsule and is separated from its fellow by little more than the dorsal edge of the septum (figs. 2 and 7, *F.S.N.*). This latter fenestra is completely covered in by the as yet somewhat ill-defined nasal bone, while the extraconchal recess (fig. 4, *E.C.R.*), a deep pit due to the inpushing of the lateral wall of the capsule to form the concha (figs. 6 and 7, *CO.*) and housing the big lateral nasal gland, is itself covered in at the side by the overlapping facial portions of the maxilla and prefrontal (fig. 2, *MAX. F.* & *PR.F*); a gap is left anteriorly however, where the facial sheet of the maxilla ceases somewhat abruptly, for the outward passage of the duct of this gland, which runs forwards to open into the nasal cavity just behind the external naris (figs. 2 and 4, *D.L.G.*).

Below and behind the extraconchal recess the facial plate of the maxilla forms a cover to the naso-lachrymal duct as it runs forwards from the orbit. The lachrymal foramen through which this duct leaves the orbit is bounded

on the outer side by the posterior edge of the facial plate of the maxilla and the very small lachrymal bone lying in contact with it, on the inner side by the outer edge of the prefrontal, which bone stands transversely across the front of the orbit.

Passing through this foramen the duct crosses above the maxillary processes of the nasal capsule (figs. 4, 6 and 7, *MX*^{1} & *MX*^{2}) and, keeping in close contact with the inner surface of the maxilla, runs forwards to open into the top of the choanal fissure below the extraconchal recess (fig. 4, *E.C.R.*).

At the back of the nasal capsule the big olfactory fenestra on either side (figs. 6 and 7, *F.OLF.*) is blocked by the olfactory bulb (fig. 2, *O.B.*), which projects into it above the sphenethmoidal cartilage (figs. 6 and 7, *SP.C.*) and planum antorbitale (figs. 3, 6 and 7, *P.A.*), the only representatives of a cartilaginous capsular wall in this region. The two olfactory bulbs form one mass supported in the mid-line, within the capsule, by the nasal septum (figs.

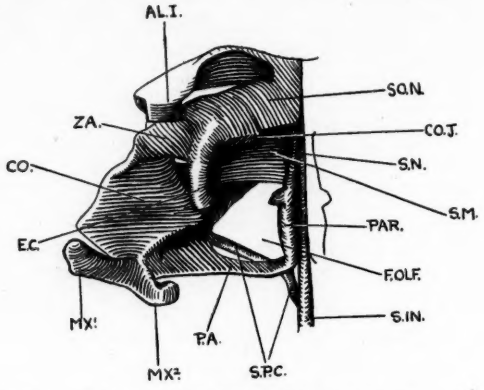

Fig. 6. Ventral view of right half of nasal capsule. $\times \frac{1}{2}$.

3, 6 and 7, *S.N.*), on either side of which the olfactory nerves run down. Below and external to each olfactory bulb the nasal capsule is shut off from the orbit by the prefrontal bone (fig. 2, *PR.F.*), met below by the dorsal plate of the palatine and laterally abutting on the inner surface of the maxilla. The dorso-lateral edge of the prefrontal is bent forwards over the roof of the capsule for a short distance, meeting the anterior end of the frontal above and the facial plate of the maxilla below; these three together form a continuous curved surface which is continued anteriorly over the roof of the capsule by the as yet ill-defined nasal.

The anterior face of the prefrontal is in contact with the planum antorbitale and covers in the gap between this and the sphenethmoidal cartilage, sending in a bony projection between the two. The ethmoidal branch of the fifth nerve passes out of the antero-mesial corner of the orbit into the nasal capsule between this projection and the sphenethmoidal cartilage; it then passes

forwards at the side of the olfactory bulb, among the roots of the olfactory nerve, and soon divides into two—a ramus lateralis passing out to the side and leaving the capsule by the foramen epiphaniale above the mouth of the extra-conchal recess, and a ramus medialis which keeps close to the bulb wall and in front of that to the septum just above the septomaxilla; this latter branch leaves the capsule by a foramen (f. apicale) in its extreme antero-mesial wall.

Viewed from the ventral surface the nasal capsule is nearly completely hidden by the premaxillae (fig. 1, *P.MAX.*) in front, the fused prevomers (fig. 1, *P.V.*) and the maxillae (fig. 1, *MAX.P.*) behind. Between these latter bones, on either side, is the cleft-like opening of the choanal fissure. These fissures are continuous behind the prevomer with the canal-like naso-palatine groove (described in connection with the palatine bone); each at first, as it runs forwards under the planum antorbitale, retains a common aperture onto the

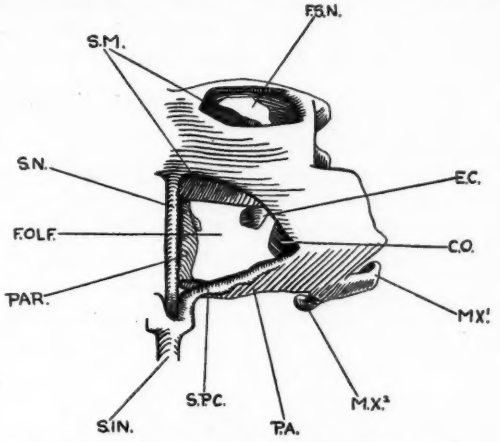

Fig. 7. Dorsal view of right half of nasal capsule. $\times \frac{1}{2}$.

palate ventral to the prevomer, but further forwards, within the olfactory region, this bone develops a ventrally directed ridge which divides the common aperture into two; further forwards still the prevomer expands ventrally into two curved plates embracing the organs of Jacobson, and the apertures of the choanal fissures swing outwards away from one another and become widely separated.

Each fissure is a cleft-like space running outwards and upwards from the buccal cavity against the inner surface of the maxilla. The ectochoanal cartilage (figs. 3, 4, 6 and 7, *E.C.*) projects back from the solum nasi along the free inner edge of the palatal sheet of the latter. Posteriorly, however, in front of the abruptly ending ventral plate of the palatine (fig. 1, *P.V.P.*) and before the fissure has swung out to the side round the organ of Jacobson, this palatal sheet of the maxilla does not extend inwards as far as the entrance of the fissure, here right in the centre of the palate, but its place is taken by a

thick mass of dense glandular tissue lying between the palatal epithelium and the ventral epithelial wall of the fissure, and probably acting as a valve for closing the latter.

So nearly in front of the anterior end of the fissure as almost to open onto the palate together with it is the duct of Jacobson's organ (fig. 1, *A.D.J.*). Immediately in front of this, below the posterior edge of the solum nasi, the prevomer and the anterior end of the maxilla approach one another. In front of this again the maxilla is replaced by the premaxilla (fig. 1, *P.MAX.*), which forms a floor to the nasal capsule in the region of the external naris and sweeps forwards and inwards round the edge of the prevomer to meet its fellow in the mid-line below the anterior extremity of the nasal septum; the palatal portions of the premaxillae thus form a horseshoe-shaped plate at the anterior end of the palate. This plate projects well in front of the nasal capsule to support the big egg-crushing tooth (figs. 1, 2 and 4, *E.*) ventrally, and dorsally to give rise to the small facial part of the premaxilla which is deflected back over the sloping anterior face of the capsule to meet the nasal.

SEPTOMAXILLA AND JACOBSON'S ORGAN

In relation to the nasal capsule there still remains to be described the septomaxilla. This membrane bone is mainly intracapsular, dividing the nasal cavity into two chambers, a smaller antero-ventral one containing Jacobson's organ and a much larger postero-dorsal one for the principal olfactory organ. The bone also possesses a very small facial portion.

The intracapsular portion (figs. 3, 6 and 7, *S.M.*) forms a sloping, slightly arched shelf over the dorsal surface of Jacobson's organ. This shelf is deflected downwards anteriorly to form a front wall also to that organ. The mesial edge of the shelf spreads out into a narrow plate at right angles to the main part and applied to the internasal septum about half-way up the side of the latter. From this edge the shelf slopes outwards and slightly downwards to rest on the inner surface of the ventro-lateral capsular wall (part of Gaupp's zona annularis) present in this region.

In front of the zona annularis arises from this outer edge of the shelf, just before the latter narrows and curves down in front of Jacobson's organ, the facial portion of the bone (figs. 2 and 4, *S.M.F.*). This is a small vertical projection running upwards to meet the processus alaris superior of the capsule (figs. 2 and 4, *P.A.S.*) and together with this completely separating the external nareal aperture (figs. 2 and 4, *E.N.*), which lies immediately below and in front of it, from another aperture (figs. 2 and 4, *D.L.G.*), which lies immediately above and behind. This latter aperture is that by which the duct of the lateral nasal gland, coming forwards along the outer surface of the capsule, enters this in order to open into the nostril (an entrance place employed among mammals by the naso-lachrymal duct).

Lygosoma at this stage does not possess a complete zona annularis such as that in Gaupp's model of *Lacerta*, but it is more nearly complete than in

Eumeces, stage 5. Corresponding to the lateral portion of Gaupp's cartilaginous ring is that region of the capsular wall (figs. 4 and 6, *Z.A.*) which projects downwards and inwards in front of the concha, with a straight posterior edge lying against the anterior extremity of the choanal fissure and an outer surface resting against the maxilla in the position occupied further back, below the concha, by that fissure itself. From the ventral edge of this part of the capsular wall projects back the ectochoanal cartilage (figs. 4 and 6, *E.C.*) described above in relation to the palatal aperture of the fissure; anteriorly its ventral edge becomes confluent with the solum nasi (figs. 3 and 6, *SO.N.*), the sole representative of a cartilaginous floor to the capsule, and thus completes the ventral part of the zona annularis; dorsally however the latter is interrupted owing to the extension of the big fenestra superior nasi (fig. 7, *F.S.N.*) into this region.

The solum nasi lies on each side on the concave dorsal surfaces of the fused prevomers and separates those bones from the downwardly bent anterior ends of the septomaxillae. Anteriorly it arises as two outwardly projecting horns from the ventral edge of the septum, but further back, within the chamber of Jacobson's organ, it becomes detached from the septum as two separate plates, from the dorsal surfaces of which arise the cartilaginous knobs constituting the conchae of the organs of Jacobson (fig. 6, *CO.J.*). The medial edges of these plates are continued back into the two paraseptal cartilages (figs. 3, 4, 6 and 7, *PAR.*) which pass back on either side of the ventral edge of the septum to the posterior extremity of the capsule, where they swing abruptly outwards and expand into the plani antorbitalia (figs. 3, 6 and 7, *P.A.*). In front of the duct of Jacobson's organ the solum nasi stops abruptly and that organ is floored in by the prevomer alone. The posterior and postero-lateral walls of the chamber are formed by the rising up of the prevomer to meet the posterior edge of the septomaxillary shelf.

Jacobson's organ is thus enclosed in a box, the walls of which are constituted as follows. The roof and anterior wall by the septomaxilla. The admedial wall: in front by the septum nasi alone, behind by the septum above and the medial ridge of the fused prevomers below. The floor: in front by the solum nasi resting on the prevomer, behind by the prevomer alone. The lateral wall: quite anteriorly by the septomaxilla, centrally by the ventro-lateral part of the zona annularis resting on the maxilla, quite posteriorly by the prevomer (in the region where the posterior end of Jacobson's organ lies mesial to the anterior end of the choanal fissure). The only apertures in this box are (*a*) for the duct of Jacobson's organ which runs onto the palate between the prevomer and the zona annularis (fig. 1, *A.D.J.*), and (*b*) for the fibres of the olfactory nerve which innervate the organ and gain access to it posteriorly between the septomaxilla and the septum nasi.

TEMPORAL AND CIRCUM-ORBITAL MEMBRANE BONES

Parietal (fig. 2, *P.*). The parietal at this stage is a narrow strip of bone lying along the dorso-lateral surface of the brain. Its posterior end forks above the

taenia marginalis, one portion passing outwards to end in contact with the anterior end of the supra-temporal over the depression between the external and anterior semicircular canals, the other, which is much shorter, keeping close to the surface of the brain above the latter and terminating in the fibrous tissue which stretches back in this region to the tectum synoticum.

In front of the supra-temporal the parietal lies just mesial to the squamosal posteriorly and the postorbital anteriorly, no temporal fossa being present as yet. The anterior end of the parietal is overlapped by the frontal.

Supra-temporal (fig. 2, *S.T.*) and *squamosal* (fig. 2, *SQ.*). These are also narrow strips of bone. Their posterior ends will be dealt with in connection with the quadrate. From that bone they curve upwards and then forwards in the same connective tissue sheath. The supra-temporal, or the innermost of the two bones, terminates shortly in front of the posterior end of the parietal which lies in the same sheath. The squamosal, or outermost of the two bones, runs forwards for some way along the lateral edge of the parietal until it is separated from that bone by the posterior end of the postorbital.

Postorbital (figs. 1 and 2, *P.O.*). This is a stout triangular plate of bone forming the posterior boundary of the orbit and with the angles drawn out into processes which lie respectively along the upper edge of the jugal, the outer edge of the frontal, and the upper edge of the squamosal.

Jugal (figs. 1 and 2, *J.*). This is a slender rod of bone encircling the orbit and meeting the postorbital behind, the transverse and maxilla in front. It is met by these last two bones about half way round the orbit but continues forwards to the front of the latter in a groove on the inner surface of the maxilla as a very slender bar which terminates between this bone and the lachrymal. Behind the point where it is met by the transverse and just above the coronoid process (fig. 2, *COR.*) of the lower jaw the jugal broadens a little and is perforated by a foramen for a small branch of the maxillary of V.

Frontal (figs. 2 and 4, *F.*). The anterior halves of the two frontals form a roof to the olfactory lobes. Behind these the bones diverge widely from each other round the back of the orbit as narrow strips overlapping the anterior ends of the parietals and meeting the post-orbital. Anteriorly they are met by the nasals in the middle line and by long backward projections of the prefrontals along their outer edges.

Prefrontal (fig. 2, *PR.F.*). The prefrontal has already been described in connection with the olfactory region. It is met by the frontal, nasal, maxilla and palatine.

Lachrymal. This is an exceedingly small plate of bone lying at the antero-lateral corner of the orbit between the naso-lachrymal duct and the inner surface of the facial portion of the maxilla at its posterior edge. It rests in front on the planum antorbitale and is met behind by the jugal. It does not come into contact with the prefrontal.

JAW ATTACHMENT

Quadrate and Stapes. The quadrate (figs. 1 and 4, *Q.*) is a large plate-like bone lying at the side of the otic region of the cranium and articulating behind with the paroccipital process (figs. 2 and 4, *P.PR.*), in front with the lower jaw. Its anterior, dorsal and posterior edges are bent over to form a semicircular rim across which is stretched the tympanic membrane. The tympanic cavity occupies the space between this membrane and the mesial plate-like surface of the quadrate, and passes downwards and inwards under the ventral edge of the latter to open into the pharynx between the pro-otic and the posterior ends of the branchial arches. The stapes (figs. 1–4, *S.*), its head inserted in the centre of the tympanic membrane, lies across the back of the tympanic cavity and passes inwards and backwards under the ventral edge of the quadrate to the fenestra vestibuli which lies in the cartilaginous region between pro-otic and opisthotic.

In its articular regions the quadrate is not yet ossified. Posteriorly it abuts on the cartilaginous paroccipital process (crista parotica) (figs. 2 and 4, *P.PR.*), but is separated from that by the posterior end of the supra-temporal (fig. 2, *S.T.*) and by a short cartilaginous spur which arises from the outer extremity of the process and projects forwards, enclosing the inpushing end of the supra-temporal between itself and the wall of the external semicircular canal. This spur corresponds to the "processus pro-oticus" of *Lacerta* and *Eumeces* (intercalare of Versluys[1]) but there is considerably less of it present in this stage of *Lygosoma*; a stout strand of fibrous connective tissue joins it to a backward projection (processus dorsalis?) of the stapes.

Shortly in front of this articular region the rolled-over dorsal edge of the quadrate is perforated by a rectangular fenestra filled with dense connective tissue into which projects the downwardly-bent posterior end of the outermost of the two temporal bones ("squamosal") (fig. 2, *SQ.*). A film of fibrous connective tissue passes from that portion of the innermost temporal bone ("supra-temporal") which is wedged between the quadrate and ear capsule forwards and outwards over the surface of the quadrate to meet the squamosal at this spot.

Just mesial to this fenestra is another smaller one, also filled by connective tissue and transmitting nothing.

From the mesial and dorsal surfaces of the quadrate and from the ventral surfaces of the squamosal and postorbital takes origin the big temporal muscle (M. capiti-mandibularis) which lies posteriorly in the cleft between the quadrate and ear capsule and passes forwards and downwards to its insertion on the lower jaw. Here may also be mentioned a smaller muscle (pterygoideus of Bradley[2], pterygoideus internus of Sanders) which is not always distinguished from the capiti-mandibularis but which in *Lygosoma* is recognisable as a separate entity inserted on the lower jaw more mesially than the above,

[1] Versluys, 1898, *Zoolog. Jahrbuch. Anat. u. Ontog.*, Bd. XII, H. 2.
[2] Bradley, 1903, *Zoolog. Jahrbuch. Anat. u. Ontog.*, Bd. XVIII.

embracing the outer surface of the epipterygoid, and taking origin from the parietal.

The nerves and blood-vessels in the region of the stapes have the usual relations to that element, to the quadrate and to the paroccipital process. The vena capitis lateralis (figs. 1 and 2, *V.C.L.*) and the hyomandibular branch of VII lie side by side in the usual groove under the paroccipital process. Just in front of the latter, ventral to the inturned end of the supra-temporal, the chorda tympani (figs. 1, 2 and 4, *CH.T.*) comes off from the hyomandibular of VII, passes out to the ventral edge of the quadrate, runs forwards in contact with this above the stapes, and finally runs down into the lower jaw near the anterior end of the quadrate in contact with the posterior extremity of the quadrate ramus (figs. 1 and 2, *PT.Q.*) of the pterygoid.

In the gap between the ramus hyomandibularis of VII, the recurrent chorda tympani, and the stapes crossing below them, runs up the stapedial artery (carotis facialis Rathke) (figs. 1 and 2, *S.A.*), a branch of the internal carotid (figs. 1 and 2, *I.C.A.*); it passes between the quadrate and the external semicircular canal and runs forwards along the ventral surface of the squamosal.

The strand of fibrous tissue connecting the processus pro-oticus with the stapes also passes down to the latter between the chorda tympani and the ramus hyomandibularis of VII; it lies in close contact with the chorda just after that nerve has branched off.

That end of the quadrate which articulates with the lower jaw is only just beginning to ossify. It lies closely applied to the dorsal surface of the articular region of Meckel's cartilage (figs. 2 and 4, *A.*), which is also only just beginning to ossify. The posterior end of the quadrate ramus of the pterygoid (figs. 1 and 2, *PT.Q.*) lies just mesial to the quadrate in this region and is connected with the ventral edge of that bone immediately behind the articular region by connective tissue; the extreme tip projects freely however, and lies in close contact with the chorda tympani, which is here just entering the pterygoideus muscle on its way to the lower jaw.

This muscle (pterygoideus Versluys, pterygo-mandibularis Bradley) (figs. 3 and 4, *M.P.*) represents the pterygoideus externus plus the pterygoideus internus; these are fused together anteriorly but separate posteriorly, where they are inserted respectively on the ventral (figs. 3 and 4, *M.P.E.*) and dorsal (fig. 4, *M.P.I.*) surfaces of the lower jaw, on the angular and posterior part of the articular. The muscle has its origin on the dorsal surface of the quadrate ramus of the pterygoid in front of the epipterygoid, on the outer surface of the base of the epipterygoid, and on the outer surface of the pterygoid more posteriorly.

The other muscles related to the quadrate ramus of the pterygoid are those which connect it with the cranium. These are the protractor pterygoidei Versluys (pterygo-sphenoidalis posterior Bradley) (fig. 4, *M.PR.PT.*) and the pterygo-parietalis (fig. 4, *M.PT.P.*).

Some of the fibres of the former take origin from the middle of the basi-

pterygoid process, the rest from the dorsal edge of the outwardly leaning processus anterior inferior of the pro-otic (figs. 1 and 2, *P.A.I.*), below the gasserian ganglion, and from the cartilaginous region of the basal plate below and in front of the processus. It is inserted along the inner surface of the pterygoid from behind the base of the epipterygoid to the posterior end of the quadrate ramus.

The pterygo-parietalis takes origin from the centre of a thickish strip of membrane which runs obliquely down the side of the brain from that part of the parietal which is level with the top of the epipterygoid to the taenia parietalis media level with the base of the latter. The muscle ensheathes the mesial and posterior borders of the epipterygoid at its lower end and is inserted along the pterygoid from the level of the anterior edge of the basal plate, forwards above the insertion of the protractor pterygoidei, to the anterior extremity of the epipterygoid; some fibres are also inserted on the ventral surface of the latter just before it reaches the pterygoid.

PALATE

Basipterygoid Processes (figs. 1 and 3, *B.P.*). From the antero-lateral corner of the basisphenoidal plate the basipterygoid process of either side runs outwards and forwards as a stout rounded bar to its articulation with the pterygoid. It reaches the latter immediately in front of the base of the epipterygoid (figs. 1, 2 and 4, *EP.*), here forms a laterally directed elbow, and before terminating bends forwards for a short distance along the ventro-medial surface of the pterygoid, with which, however, it never comes into very close contact.

Where it leaves the basis cranii the basipterygoid is completely ossified, but this ossification does not extend out as far as the elbow, the distal half of the process being completely cartilaginous. At its proximal end the process is crossed by the big vena capitis lateralis (fig. 1, *V.C.L.*), which runs outwards and upwards above it as it passes back from the infra-orbital sinus. The palatine branch of VII (fig. 1, VII, P^2) having issued from the Vidian foramen just mesial to the base of the basipterygoid, runs forwards and outwards along the dorso-medial surface of the latter onto the dorsal surface of the palate.

Pterygoid (figs. 1 and 3, *PT.*). In front of its articulation with the basipterygoid the pterygoid spreads out into a thin plate below the back of the eye and forms the hinder margin of the bony ring surrounding the large suborbital fenestra (fig. 1, *F.SUB.*), a ring completed by the transverse, maxilla and palatine. The pterygoid forms about a third of the inner boundary of the fenestra and then meets the palatine and narrows to form a short process inserted between the upper and lower plates of the latter.

Palatine (figs. 1 and 2, *PAL.*). When the skull is viewed from below the palatines are seen as two sheets of bone running side by side down the centre of the palate between the suborbital fenestrae, and swinging out round the anterior margins of these to meet inward projections of the maxillae. The inner

edges of these plates approach each other very closely in the mid-line and form a kind of secondary palate, since they almost completely shut off the naso-palatine groove from the main part of the buccal cavity, and indeed the flaps of buccal epithelium in which they lie extend beyond the bone and actually overlap each other, appearing to form a kind of valve. This inner edge of either palatine is continued back behind the pterygoid articulation as a narrow bar diverging somewhat from its fellow and lying alongside the inner edge of the pterygoid but separated from that bone by a cleft filled with connective tissue. This bar and the medial edge of the pterygoid alongside it, and for a short distance behind it, both lie in a backward extension of the epithelial flaps mentioned above, but the flaps in this region do not nearly approach each other, the naso-palatine groove being in wide communication with the buccal cavity.

From the upper surface of each of the ventral palatine plates described above arises another thin bony plate arching upwards and inwards at an angle of about 45° over the naso-palatine groove and making the palatine bone Y-shaped in transverse section. This dorsal plate of the palatine (fig. 1, *P.D.P.*) becomes more and more prominent as it passes forwards and here forms a flat surface with the outer, suborbital edge of the palatine (the limb of the Y), whereas the ventral plate in the secondary palate appears as a slightly bowed downward projection of this surface.

The palatine branch of VII (figs. 1–7, VII, P^2), running forwards along the dorsal surface of the pterygoid and palatine, passes gradually from the outer to the inner edge of the latter and, towards the front of the orbit, comes to lie in a groove formed by the bending upwards of the mesial edge of the dorsal palatine plate on either side of the base of the interorbital septum. Right at the anterior extremity of the orbit the floor of this groove becomes bent down to form a regular gutter.

At the level of the planum antorbitale both dorsal and ventral plates of the palatine cease abruptly, but a slender process from the mesial edge of the former runs forwards for some way in a canal in the prevomer and thus supports the palatine anteriorly at its inner edge, the maxillary articulation supporting it at its outer edge; the choanal fissure opens into the naso-palatine groove between these two articulations.

Transverse (figs. 1 and 2, *T.*). The transverse is a small plate of bone running inwards and backwards from the maxillo-jugal articulation to the pterygoid and forming with the short transverse ramus of the latter the postero-lateral boundary of the large suborbital fenestra. Its articulation with the pterygoid is of the type characteristic of the whole palate, inasmuch as it forms a sheath round the narrow distal extremity of the transverse ramus of that bone.

Maxilla. The zygomatic part of this bone (fig. 2, *MAX.Z.*), forming the anterior half of the zygoma and the antero-lateral border of the suborbital fenestra, is met behind by the transverse and jugal. A double row of teeth extends right along the outer edge of the bone to its posterior end in this

region. In the palate the maxilla does not play any very great part, its palatal portion (fig. 1, *MAX.P.*) being a rather narrow strip projecting inwards as a thin shelf from the tooth-bearing region; this shelf meets the palatine in front of the suborbital fenestra and thence runs forwards with a free inner edge to meet the premaxilla anteriorly; at its extreme anterior end, in front of the duct of the Organ of Jacobson and immediately behind the palatal portion of the premaxilla, it comes into contact with the prevomer.

The facial portion of the maxilla (fig. 2, *MAX.F.*) extends upwards in front of the orbit as a thin sheet forming an outer wall to the extraconchal recess (fig. 4, *E.C.R.*). The posterior edge of this portion comes into contact with the prefrontal (fig. 2, *PR.F.*) which stands at right angles to it as the front wall of the orbit; the naso-lachrymal duct passes through a gap between the two bones.

The relations of the maxilla to the nasal capsule and choanal fissure have been dealt with in more detail elsewhere.

Prevomer (fig. 1, *P.V.*). The two prevomers are completely fused at this stage. They form a rather complex bone occupying the central part of the palate anteriorly, between the palatal apertures of the choanal fissures. Posteriorly they articulate with the palatines as described above, anteriorly they meet the premaxillae. The dorsal surface of the joint bone has a complex arrangement of grooves and ridges in relation to the other structures in contact with it—i.e. to the articulatory processes of the palatines, the nasal septum, the paraseptal cartilages, and the Organ of Jacobson.

Premaxilla (figs. 1 and 2, *P.MAX.*). The palatal portions of the premaxillae form a horseshoe-shaped plate round the anterior edge of the fused prevomers. The limbs of the horseshoe meet the maxillae behind. Anteriorly the right premaxilla supports the big egg-crushing tooth (figs. 1, 2 and 4, *E.*), and as this lies symmetrically in the mid-line the right premaxilla in this region encroaches on the left side and the palatal exposure of the left premaxilla is narrower anteriorly than that of the right.

HYOID AND BRANCHIAL ARCHES

These are essentially similar to those of the 47 mm. *Lacerta* embryo figured by Gaupp[1]. The free dorsal extremity of the hyoid bar (figs. 2, 3 and 4, *H.*) lies well below the posterior end of the quadrate at this stage, and has no connection with either stapes or paroccipital process. The plate-like expansion of the hyoid arch (figs. 2, 3 and 4, *H.P.*) just posterior to the point where it bends sharply back after a short forward course from the mid-ventral line is even larger than in *Lacerta*: the outer edge of the plate is in contact with the ventral surface of the big pterygo-mandibularis muscle (fig. 3, *M.P.* and fig. 4, *M.P.E.*) enfolding the lower jaw in this region.

The first branchial arch (figs. 2, 3 and 4, *B.* 1.) is slightly longer than the hyoid; their dorsal ends are in close proximity. This arch is ossified or beginning

[1] Gaupp, 1905, *Hertwig's Handbuch*, Bd. III. ii. Die Entwickelung des Kopfskelets.

to ossify along the greater part of its length. The second branchial arch (figs. 2 and 3, *B.* 2.) is, as in *Lacerta*, very short.

The same additional sickle-shaped piece of cartilage (figs. 2, 3 and 4, *Bx.*) as Gaupp interprets as the separated dorsal extremity of the second branchial arch is present in the branchial region, lying just posterior to the dorsal ends of the hyoid and first branchial. It does not lie parallel to these but rather within and at an angle to them, with its upper, handle-like end directed straight upwards close against the opisthotic where that forms the outer wall of the posterior ampullary recess—i.e. some way behind the paroccipital process.

The hypoglossal nerve (figs. 1 and 2, XII) leaves the skull just posterior to this cartilaginous bar and runs downwards and forwards along its outer surface, giving off a branch which loops round the back of it to the genio-hyoid muscle. The main hypoglossal nerve runs on in front of this cartilage close to the first branchial arch, first on its ventral and then on its lateral surface.

The vena capitis lateralis (figs. 1 and 2, *V.C.L.*) crosses external to the upper end of the accessory branchial cartilage, the internal carotid artery internal to its lower end in the loop of the sickle.

LOWER JAW

The lower jaw is of the normal lacertilian type. Meckel's cartilage, except in the articular region, is at this stage already entirely sheathed by membrane bones. The dentary supports a double row of teeth, similar to those on the maxilla, the inner row alternating as there with the outer row, which are the larger.

In conclusion I wish to express my thanks to Prof. J. P. Hill for enabling me to carry out the work during my tenure of the Percy F. Macgregor Scholarship in Zoology, and for allowing me free access to his embryological material for comparative purposes.

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LIST OF ABBREVIATIONS USED IN FIGURES

A. articular; *A.D.J.* aperture for duct of Jacobson's organ; *A.L.I.* processus alaris inferior; *A.V.S.C.* anterior vertical semicircular canal; *B.*1. 1st branchial arch; *B.*2. 2nd branchial arch; *Bx.* accessory branchial cartilage; *B.F.* basicranial fenestra; *B.P.* basipterygoid process; *B.S.* basisphenoid; *CH.T.* chorda tympani; *CO.* concha; *CO.J.* concha of Jacobson's organ; *COCH.* pars cochlearis of ear; *COR.* coronoid; *D.L.G.* entrance place of duct of lateral nasal gland; *D.P.I.* and *D.P.I.*[1] depressor palpebrae inferioris; *E.* egg-tooth; *E.C.* ectochoanal cartilage; *E.C.R.* extraconchal recess; *E.H.S.C.* external horizontal semicircular canal; *E.N.* external naris; *EP.* epipterygoid; *F.* frontal; *F.O.* fenestra optica; *F.OLF.* fenestra olfactaria; *F.S.*[1], [2]*F.S.*[2], *F.S.*[3] fenestrae septi; *F.S.N.* fenestra superior nasi; *F.SUB.* fenestra suborbitalis; *G.G.* gasserian ganglion; *H.* hyoid arch; *H.P.* hyoid plate; *I.C.A.* internal carotid artery; *J.* jugal; *L.P.M.* left

premaxilla; *M.A.R.*, *M.A.R.*[1], *M.A.R.*[2] internal rectus; *MAX.F.* facial sheet of maxilla; *MAX.P.* palatal sheet of maxilla; *MAX.Z.* zygomatic part of maxilla; *M.E.R.* external rectus; *M.I.O.* inferior oblique; *M.I.R.*, *M.I.R.*[1] inferior rectus; *M.P.* pterygoideus; *M.P.E.* external insertion of pterygoideus; *M.P.I.* internal insertion of pterygoideus; *M.PR.PT.* protractor pterygoidei; *M.PT.P.* pterygo-parietalis; *M.R.B.* retractor bulbi; *M.S.O.* superior oblique; *M.S.R.* superior rectus; *MX.*[1], *MX.*[2] maxillary processes; *O.L.*, *O.B.* olfactory lobes; *P.* parietal; *P.A.* planum antorbitale; *P.A.I.* processus anterior inferior of pro-otic; *PAL.* palatine; *PAR.* paraseptal cartilage; *P.A.S.* processus alaris superior; *P.D.P.* dorsal plate of palatine; *P.F.* pituitary foramen; *P.M.* pila metoptica; *P.MAX.* premaxilla; *P.O.* postorbital; *P.P.* pila pro-otica; *P.PR.* paroccipital process; *PR.F.* prefrontal; *P.S.* presphenoidal cartilage; *PT.* pterygoid; *PT.Q.* quadrate ramus of pterygoid; *P.V.* prevomer; *P.V.P.* ventral plate of palatine; *P.V.S.C.* posterior vertical semicircular canal; *Q.* quadrate; *R.S.T.* recessus scala tympani; *S.* stapes; *S.A.* stapedial artery; *S.IN.* septum interorbitale; *S.M.* septomaxilla; *S.M.F.* facial process of septomaxilla; *S.N.* septum internasale; *SO.N.* solum nasi; *SP.C.* sphenethmoidal cartilage; *SQ.* squamosal; *S.SUP.* solum supraseptale; *S.T.* supra-temporal; *T.* transverse; *T.M.*[1] posterior end of taenia marginalis; *T.M.*[2] anterior end of taenia marginalis; *T.P.M.* taenia parietalis media; *V.C.L.* vena capitis lateralis; *V.F.* Vidian foramen; *Z.A.* lateral part of "zona annularis."

Nerves. II, III, IV, V *OP.*, V *MAX.*, V *MAN.*, V *TEM.* (r. temporalis maxillaris), VII P^1 and VII P^2 (r. palatinus), *CH.T.* chorda tympani, XII.

A NOTE ON THE POST-CORONAL SULCUS, WITH DISSECTIONS OF THE EPICRANIAL APONEUROSIS IN TWO CASES OF ITS OCCURRENCE

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In connection with the collection of West Scottish Skulls preserved in the Anatomical Museum of Glasgow University and previously described by Dr Matthew Young(1), it was known that a feature of the series was the presence in many specimens of a post-coronal sulcus running transversely across the skull behind the bregma. On reviewing the whole series with a view to determining the frequency of its occurrence, I find the groove to be present in 238 cases out of a total of 710 crania examined—i.e. in 33½ per cent. The incidence does not appear to vary to any appreciable extent in the two sexes, but is much greater among metopic skulls and the groove is on the average more pronounced in skulls of this type. In 40 adult metopic skulls the groove is present in 27 cases (67½ per cent. occurrence). In 480 adult non-metopic skulls, 147 or 30⅝ per cent. are grooved.

What is the cause of this sulcus? In his book on the muscles of the trunk, Eisler(2) describes the presence of transversely-running bands of fibres in the epicranial aponeurosis, and he suggests in passing, without however giving any proof of this view, that the presence of such fibres may cause grooving of the cranial vault. Under the direction of Professor Bryce, I undertook dissections of the scalp in order to obtain first-hand evidence regarding the course of the fibres in the epicranial aponeurosis, and in particular to find if any causal relationship could be established between the presence of transverse bands and the post-coronal sulcus. Mounted needles were largely used in cleaning the fibres, and the dissection was aided by a stereoscopic magnifier.

In the first specimen dissected there was no trace of a post-coronal groove, but a fine band of fibres was found crossing the mid-sagittal line transversely in the position in which the groove occurs. The question then was whether such a band, only more pronounced in character, occurred in cases of post-bregmatic grooving.

Subsequently, two subjects with well-marked grooves came into the Anatomy Rooms, and their scalps were dissected (specimens *A* and *B* illustrated). In both cases, strongly-marked transverse fibres occupied the post-coronal sulcus, the antero-posterior limits of the depression coinciding with those of the pronounced transverse tendinous band. After the dissection had been completed in each case, the skull-cap, with scalp attached, was removed in order to determine whether the groove on the outer side was reflected in any

way on the inner table, and in one case (specimen *A*) a plaster-cast was made of the interior of the skull-cap. In neither case was there any definite marking within corresponding to the groove without.

The following is a detailed account of the dissections, and for purposes of contrast a description of the normal (non-grooved) specimen is first given (Plate I, fig. 1).

The main band of aponeurotic fibres sprang from the upper margin of the occipitalis muscle on either side, and passed upwards and forwards over the parietal eminence with a distinct medial inclination. The fibres became finer as they passed forwards, and a short distance in front of the parietal eminence each band expanded somewhat. The bulk of the fibres ran forwards into continuity with the muscle fibres of the frontalis (the longest fibres of which reached practically to the coronal suture), so that the main "run" of the aponeurotic band was in an oblique line from behind, forwards and inwards, with a slight medial convexity. In addition, on the lateral but especially on the medial side of each band, other fibres took divergent courses. On the lateral side posteriorly, some fibres turned with a shorter medial convexity so as to run into the auricularis posterior muscle, while further forwards the fibres from the auricularis superior appeared to sweep forwards, joining the main aponeurotic band. On the medial side, several bunches of fibres turned inwards towards the middle line, but only one band actually crossed over to be continued into a corresponding band from the other side. This band, less than half an inch in antero-posterior width and composed of very delicate fibres, crossed the middle line just behind the coronal suture. In the case of the other medially-turned bundles, the fibres spread out from each other and terminated at varying distances from the middle line, being more firmly attached to the overlying fascia towards their free ends. As these bands were dissected out, the appearance was exactly as if a thin sheet of fibres crossing the vertex from side to side had been burst, except at the one point, by the cranial expansion. Behind, between the occipitales muscles and the posterior ends of the lateral tendinous bands, the interval was filled by a layer of soft dark red fibrous tissue, the fine fibres running antero-posteriorly.

Specimen A. (Plate I, figs. 2, 3.) The skin and superficial fascia of the scalp were very much finer than in the previous specimen; there was a well-marked post-coronal depression. As before, the aponeurotic layer commenced posteriorly on either side as a broad band springing upwards from the occipitalis muscle. A more distinct accession of forwardly-turning fibres from the auricularis superior muscle was present. Only a small part of each lateral band became continuous with the frontalis muscle, the greater part turning medially, forming a broad transverse band crossing the vertex in the middle line from about $\frac{1}{2}$ in. in front of the coronal suture to about 3 inches behind it. The fibres crossing in the depression formed a distinctly firmer band about 1 inch in width, and interlaced in the middle line. Immediately in front of the coronal suture the transverse fibres abruptly thinned off, and less abruptly

behind, where a fine, smooth band about 2 inches broad swept over from side to side without any marked interweaving in the middle line. Numerous small spindle-shaped slits occurred in the transverse band, transmitting minute blood-vessels. The transverse band was not fixed to the underlying bones, and could be made to glide over the skull in a lateral or antero-posterior direction. (This mobility has disappeared since preserving the specimens in alcohol.) Anteriorly, a distinct band of fibres passed from the adjacent borders of the frontalis and auricularis muscles medially and slightly posteriorly, deep to the main antero-posterior band, to take part in the formation of the transverse band lying in the post-coronal sulcus. Except for the gap between the occipitales muscles, the appearance in this subject was rather that of a continuous band of muscle fibres running from the periphery upwards towards the vertex. The frontales muscles were very distinctly confluent across the middle line, and their longest fibres reached to within $1\frac{1}{4}$ inches of the coronal suture. On removing the skull-cap, the dura mater was observed to be rather more adherent than usual to the cranial vault. No transverse ridge corresponding to the groove outside was found on the inner table of the bone, and a plaster-cast taken of the interior of the skull showed an uninterrupted convexity along the mid-sagittal line.

Specimen B. (Plate II, figs. 4, 5.) The occipitalis muscle was rather broader than usual, and towards the auricle blended with the auricularis posterior. As in the other specimens, a band of relatively coarse aponeurotic fibres, about 2 inches broad, passed upwards, forwards and inwards from the upper border of the occipitalis, sweeping over the parietal eminence, the fibres becoming finer as they went forwards. At that point the fibres on the inner border of the band turned more abruptly inwards and disappeared towards the middle line of the head. Further forwards, the band was broadened by the addition of finer fibres passing upwards and forwards from the auricularis superior muscle, and about an inch in front of the parietal eminence the aponeurotic fibres diverged into two streams. One passed obliquely forwards and inwards, radiating out into a fan-shaped expansion attached to the upper border of the frontalis muscle. The other band of fibres, about 2 inches broad, passed transversely over the top of the cranium, continuing into the corresponding fibres of the other side, and decussating slightly in the middle line. It occupied a transverse groove, the floor of which was deepest anteriorly just behind the coronal suture and gradually rose posteriorly to resume the general convexity of the cranium at a point mid-way between the parietal eminences. In front of the coronal suture was a rounded eminence lying in the triangle formed by the anterior border of the transverse band and the inner borders of the anterior radiations. The dura mater was even more adherent to this skull-cap than in specimen *A*. The inner table showed a very irregular surface and, in spite of an elongated bulging along the anterior part of the sagittal sinus groove, displayed no ridge corresponding to the depression on the outer table.

Fig. 1.

Fig. 1. Normal (non-grooved) skull, viewed from above.

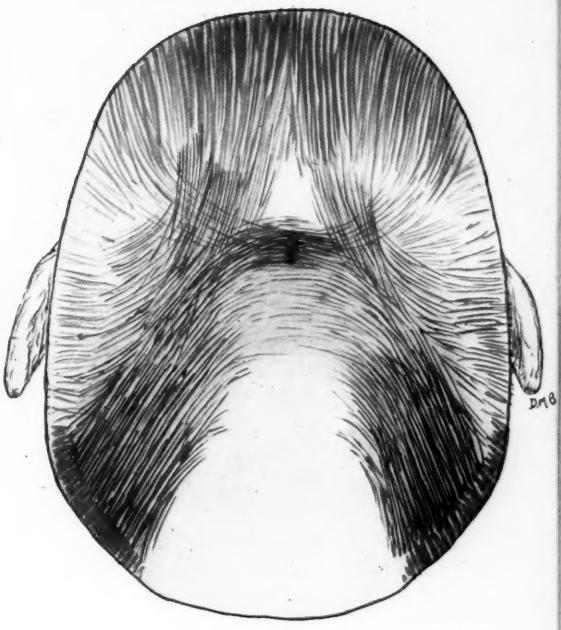

Fig. 2. Skull with narrow groove (specimen *A*), viewed from above.

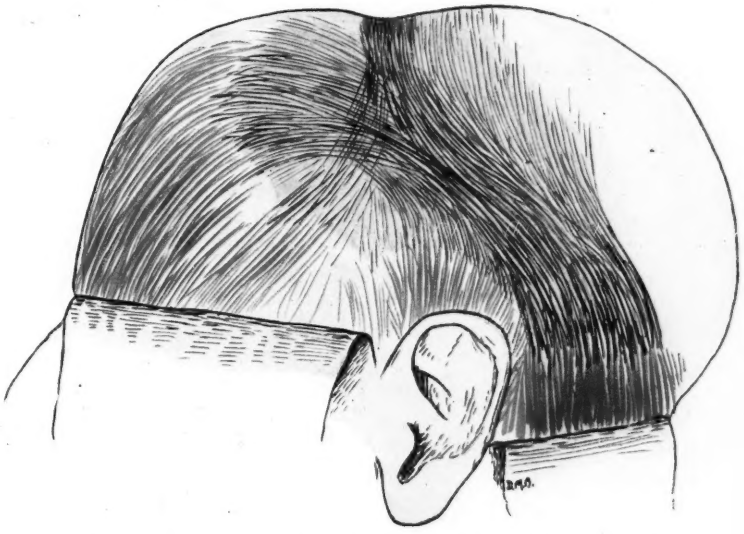

Fig. 3. Skull with narrow groove (specimen *A*), viewed from the side.

Were the post-coronal sulcus due to an intra-cranial cause, it would be reasonable to expect an exaggerated reversal within of the groove on the outside, but in both the specimens dissected, the smooth, transverse depression appears to be purely a feature of the outer table of the skull, and it is therefore suggested that its presence may be caused by the persistence of the unusually strong transverse band of the epicranial aponeurosis which, in both these cases, was found to be within it.

It is interesting to note the prevalence of this post-coronal sulcus in skulls of the West Scottish type, as exemplified in the Glasgow University Collection. The greater incidence among metopic skulls is also a striking feature. As already pointed out, the depression occurs in the majority of such skulls and more than twice as frequently as in the non-metopic variety.

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THE NERVES OF THE HUMAN LARYNX

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In 1884 Exner published a paper on the nerves of the larynx. It was based on experimental work and on dissection. His experiments were of two types: they consisted of (1) cutting the laryngeal nerves of dogs and rabbits and months later killing the animals and noting what muscles had degenerated. (2) Stimulating the nerves and noting what muscles contracted. His dissections consisted of the microscopic examination of three larynxes of newly-born children. One of these he cut into 150 serial sections and the other two he used for determining minute or obscure points.

On this work he showed that the innervation of the larynx was much more complicated than had been previously thought. He showed that the superior laryngeal nerve was not a purely sensory nerve and that the inferior laryngeal was not purely motor. He furthermore discovered in rabbits a new nerve which he called the middle laryngeal.

His results were opposed by Onödi, whose work I have not been able to use. But Nicolas in Poirier and Charpy (1903) follows Exner's description, even reproducing two of his diagrams.

Exner's description seems to be the popular one on the Continent; on the other hand, English speaking anatomists follow the older and more classical description.

The differences between the two descriptions are very great. The classical description restricted the internal laryngeal to a purely sensory function. The other teaches that each laryngeal muscle has a double nerve supply from the superior and from the inferior laryngeal nerves.

The description given here is based on naked eye dissections of 33 adult larynxes. Ten of these were used for microscopic work after the nerve supply of the arytenoideus had been worked out (Bielchowsky's method was used), but as this work did not give satisfactory results, the remaining 23 were not sectioned. The distribution of the other nerves was worked out in addition to the arytenoideus in these specimens.

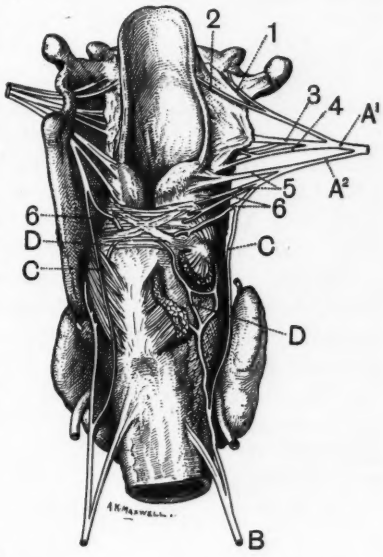
THE EXTERNAL LARYNGEAL NERVE

A branch of the superior laryngeal, variable in size, generally small. It runs downwards and forwards, deep to the sterno-thyroid and close to this muscle's attachment to the thyroid cartilage. The corresponding artery is superficial to the muscle.

At first it lies on the inferior constrictor, but as it approaches its termination it passes deep to the inferior constrictor and lies on the thyroid cartilage.

The nerve passes under those fibres of the inferior constrictor which are attached to the inferior tubercle of the thyroid cartilage.

The nerve winds closely round this tubercle, enters the crico-thyroid muscle on its superficial surface where it breaks up into its filaments for the supply of the muscle. There are two possible explanations of its close relationship to the inferior papilla. (1) That the nerve is pulled round this to supply the reflected part of the muscle which is attached to the internal surface of the thyroid cartilage; (2) that filaments go to join the inferior laryngeal nerve. In two specimens I have found such filaments, but they are exceedingly small and difficult to find; they join the inferior laryngeal as it passes over the crico-arytenoideus lateralis.



As the nerve passes deep to the inferior constrictor muscle, it gives off a constant twig to the muscle and two other inconstant twigs.

(1) To the apex of the lateral lobe of the thyroid gland.

(2) A branch which passes upwards to the region of the superior tubercle of the thyroid cartilage. In three larynxes out of 23 this nerve passed through a foramen in the cartilage. In two it ended in the cartilage and no foramen was found.

This foramen was present twice on the left side, once on the right. In a fourth specimen it was present on both sides and in this specimen it contained an artery. The foramen in this specimen was larger than in the other cases. The artery was apparently that branch of the superior thyroid which is stated to accompany the internal laryngeal nerve, but which really enters the larynx through the thyro-hyoid membrane on a lower plane quite close to the thyroid cartilage. When the nerve passed through the foramen it joined the internal laryngeal nerve.

THE INTERNAL LARYNGEAL NERVE (fig.: A^1 and A^2)

The internal laryngeal nerve enters the larynx through the thyro-hyoid membrane. As already mentioned, the artery enters the larynx on a lower plane quite close to the superior border of the thyroid cartilage and separately from the nerve.

While it is in this membrane it divides into two main divisions. One, the larger, runs horizontally inwards towards the mesial plane (fig.: A^1). The

other runs downwards through the sinus pyriformus, in the aryteno-epiglottic fold deep to the mucous membrane (fig.: A^2).

This latter branch is the one usually called the internal laryngeal but it is less than half the internal laryngeal. The other is referred to as a leash or sheaf of fine filaments. This sheaf can be reduced to a simple and fairly constant plan. It will be found to consist of four main twigs which give off many secondary twigs (fig.: 1, 2, 3, 4).

The first turns upwards immediately it gets through the membrane. Sometimes it appears before the main nerve pierces the thyro-hyoid membrane. It runs upwards in the membrane to be distributed to the mucous membrane of the lateral wall of the pharynx and lateral to the glosso-epiglottic fold. The second passes mesially and upwards to sink into the anterior surface of the epiglottis just mesial to the attachment of the glosso-epiglottic fold. It supplies the mucous membrane in the vallecula.

The third runs horizontally inwards and ends on the anterior surface of the epiglottis quite close to its fellow of the opposite side. The epiglottis is getting narrow at this level which is just below the superior border of the thyroid cartilage. This twig gives branches to the mucous membrane of the vestibule.

The fourth passes downwards and mesially to end on the anterior surface of the epiglottis close to the attachment of the thyro-arytenoid and thyro-epiglottic muscles. It supplies the mucous membrane of the false vocal cord and the region just above it.

Three of these twigs, it will be noted, end definitely on the epiglottis.

THE DESCENDING DIVISION OF THE INTERNAL LARYNGEAL (fig.: A^2)

This runs down in the mesial wall of the sinus pyriformis giving off two or three branches, to the muscles in the aryteno-epiglottic fold, to the mucous membrane, and to the mucous glands on the posterior surface of the arytenoid cartilage (fig.: 5).

Then it gives one and sometimes two branches to the inter-arytenoideus muscle. This branch was present in 31 out of 33 specimens—so I venture to say it is quite constant. It sinks into the posterior surface of the muscle just above the oblique part of the muscle, arising from the arytenoid cartilage of the same side (fig.: 6).

It goes right through the muscle and can be found to end on the posterior surface of the cartilage; before it does so, it gives definite twigs to the muscle and frequently a little twig to join the branch coming to this muscle from the recurrent laryngeal nerve. The nerve is then continued down on the posterior surface of the arytenoideus posticus deep to the mucous membrane, lying in a well-marked layer of connective tissue; here it gives off many fine twigs to the mucous membrane but none to the posterior surface of the crico-arytenoideus posticus as Exner states.

It ends by piercing the inferior constrictor and joins the inferior laryngeal

outside the larynx. This is usually described as being the ramus communicans superior joining the ramus communicans inferior of the recurrent laryngeal. But it is difficult to say where one begins and the other ends. There is no anastomosis to mark out their junction and I describe it as above to suggest a continuous nerve. On the other hand, it might be looked on as a continuation of the inferior laryngeal upwards (fig.: *C*).

THE INFERIOR OR RECURRENT LARYNGEAL NERVE (fig.: *B*)

The right nerve lies more anteriorly on the trachea than the left, but on each side they enter the larynx at the same place. Each nerve gives off branches to the trachea and oesophagus in its course upwards.

About an inch before it enters the larynx it divides into two divisions and also at about the same place it gives off two other fairly constant fine twigs. One goes to the thyroid gland where this is attached to the trachea, the other makes for the oesophagus just below its angle of junction with the pharynx.

Of the two main divisions, one is the branch which unites with the internal laryngeal. It is the branch already described as the continuation of the internal laryngeal. It can be picked up before it enters the larynx. It is the smaller of the two. It enters the larynx by piercing the inferior constrictor at the angle of junction of the oesophagus with the pharynx. The larger division lies more laterally. This pierces that part of the inferior constrictor which arises from the cricoid cartilage, immediately behind the articulation of the inferior cornu of the thyroid with the cricoid. It is the muscular division of the nerve. Branches of the inferior thyroid artery are in close relation with the nerve, as it enters the larynx, the artery being on a more anterior plane but some of its branches may pass behind the nerve.

In the Larynx:

The course of the smaller division has already been described.

The larger division, or muscular division.

It runs upwards at the lateral border of the crico-arytenoideus posticus muscle as far as its attachment to the muscular process of the arytenoid cartilage. In this part of its course it first of all gives off a branch to the crico-arytenoideus posticus muscle which enters the deep surface of the muscle. It then gives off a twig which passes deep to the crico-arytenoideus posticus muscle to appear at its upper border and then enter the posterior surface of the inter-arytenoideus muscle. This is the branch of supply from the inferior laryngeal nerve. As it lies deep to the arytenoideus posticus, it is joined by a twig which winds round the groove on the posterior surface of the cricoid cartilage immediately below the crico-arytenoid articulation. This twig comes from the main part of the recurrent nerve (fig.: *D*). In this way it is seen that the inter-arytenoideus muscle gets a double nerve supply on each side. The branch from the recurrent laryngeal is frequently joined to the branch from the internal laryngeal of the same side. Neither nerve goes across the mesial plane to the opposite side.

The twig from the inferior laryngeal nerve ends in a different manner to that of the internal laryngeal. It breaks up very quickly into its filaments of distribution and does not go through the muscle to end on the cartilage. This nerve can be quite easily picked up as it appears at the upper border of the crico-arytenoid posticus, in the little triangular space bounded by the mesial plane, the crico-arytenoid and inter-arytenoideus muscles. As already stated this double nerve supply seems to be constant.

The inferior laryngeal nerve then lies on the superficial surface of the crico-arytenoideus lateralis. Here I have twice seen it joined by a small twig from the external laryngeal nerve. It gives fine twigs to this muscle and then ends by sinking into the thyro-arytenoid muscle. Here I have seen it joined by a twig from the internal laryngeal nerve.

To sum up there are four ways of looking at the laryngeal nerves:

(1) The classical way, following Luschka, that they are separate sensory and motor nerves.

(2) The school of Exner which says they are mixed motor and sensory nerves and that each muscle receives a double nerve supply.

(3) An obvious middle way which says that the nerves are mixed nerves but which denies that all the muscles have a double nerve supply. This is what I found: that the arytenoideus was supplied by the internal and recurrent laryngeal nerves, but that the rest including the crico-arytenoideus posticus had only a supply from the recurrent laryngeal. This fits in with the pathological facts.

(4) It seems to me however that such an explanation does not fit in with all the facts. For example, the connections between the various nerves. So I suggest that the laryngeal nerves are really a plexus of nerves. Just as the vagus breaks up into its various plexuses in the body, it does the same in the larynx. It is a highly modified plexus. I would further suggest it arose by the larynx separating a strand of fibres from the vagus—that this strand is represented by the continuous nerve joining the internal and recurrent laryngeal, and that the separation from this strand of further fibres forms the various nerves of the larynx.

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ABNORMAL POSITION OF THE ILIAC AND PELVIC COLONS

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During the dissection of the abdomen in a Sudanese negro the following remarkable displacement of the iliac and pelvic portions of the colon was discovered.

The descending colon occupied its normal position and measured 24 cms. in length.

About 1½ inches above the anterior superior spine of the ilium, the colon bent sharply upon itself and ascended parallel to the descending portion and overlying it, so that the descending colon was quite hidden in the undisturbed condition. This ascending portion passed upwards as high as the transverse colon, close to the lower border of the spleen, where it once more turned upon itself and again descended parallel and medial to the ascending part just described, and passing over the pelvic brim became continuous with the rectum. The combined length of these two parts, which may be considered to represent the iliac and pelvic portions of the normal colon, measured 58 cms. and both were covered by the general peritoneal layer of the posterior abdominal wall, which formed a short mesentery, continuous with the peritoneum covering the descending colon proper, and passing thence over the ascending portion of the loop, dipping between it and the descending part of the loop where it was attached to the posterior abdominal wall, and then crossing this descending part to become continuous with the peritoneum forming the mesentery of the small intestine. Both these portions of bowel were uncovered posteriorly and were loosely attached by connective tissue to the posterior abdominal wall.

The upper end of this great loop was attached by extra-peritoneal tissue to the transverse meso-colon, and medially to the duodenum at its junction with the jejunum.

At the point in the left iliac fossa where the descending colon proper terminated, the taeniæ coli gave place to a continuous layer of longitudinal muscular fibres, which were carried uninterruptedly throughout the remainder of the bowel into the longitudinal muscle of the rectum.

The attached sketch illustrates the appearance and position of the loop, except that in the undisturbed condition, the descending colon proper was completely hidden by the ascending part which overlaid it. The loop was evidently of congenital origin and not due to secondary adhesions.

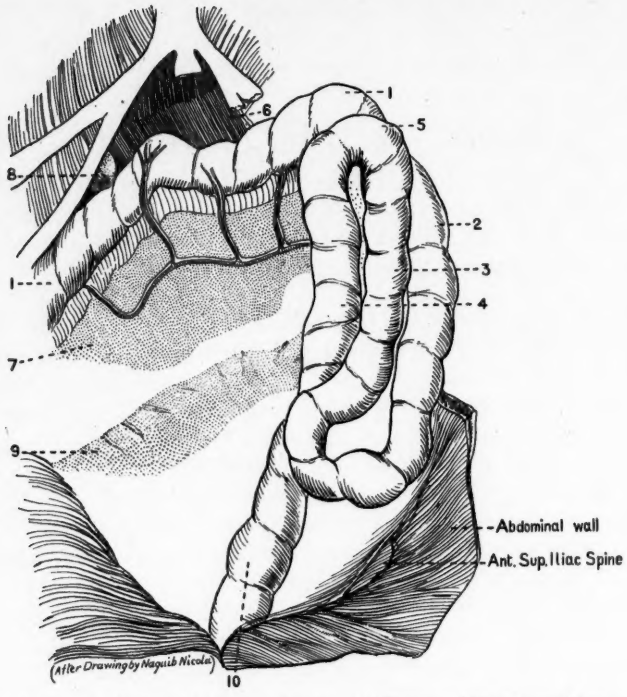

Diagram to show an abnormal position of the Sigmoid Flexure. 1 Transverse Colon, 2 Descending Colon, 3 and 4 Iliac and Pelvic portions of Large Intestine, 5 Sigmoid Flexure, 6 Exposed portion of Liver, 7 Transverse Meso-colon, 8 Fundus of Gall-bladder, 9 Remainder of mesentry of Coils of Small Intestine, 10 Going to Rectum.

REVIEWS

The Origin of Milk Glands: The Mammary Apparatus of the Mammalia, in the Light of Ontogenesis and Phylogenesis. By ERNST BRESSLAU, M.D., late Professor of Zoology in the University of Strassburg. With a Note by Prof. J. P. HILL, F.R.S. pp. 145. Figs. 47. (London, Methuen and Co., Ltd.) 1920.

Prof. J. P. Hill, in a note introducing the above volume to English readers, makes the statement that this work of Professor Bresslau's has lost nothing of its value by its corrected proofs having to wait six years before being issued from the press. With this statement we agree most cordially. For the first time a rational and simple explanation of the origin of milk glands is given—one founded on a prolonged investigation of original material. This book, which contains the substance of three lectures given by Prof. Bresslau at University College, London, in the spring of 1913, traces the origin of the mammary apparatus of monotremes, marsupials and Eutherian mammals to a common source—the brooding organs of the primitive mammalian ancestry. The story is clearly and fully told with the result that a chaotic mass of facts has been given an orderly sequence. We commend this work to the attention, not only of all anatomists but of all medical men.

Initiative in Evolution. By WALTER KIDD, M.D., F.R.S.E. 80 original illustrations. pp. 262. (London, H. F. and G. Witherby.) 1920. Price 15*s.* net.

If this notice of Dr Walter Kidd's greatest contribution to our knowledge of the hair patterns of mammals is somewhat belated, the delay is in no way due to a lack of appreciation of its importance and worth. On the contrary, no one can give serious attention to the new facts which are set out in the *Initiative in Evolution* without recognising its author as a student and investigator of the best kind—one who has made himself master of a definite field of knowledge. It may be thought that hair patterns—the directions in which the hairy coverings of mammals are arranged—is a somewhat limited subject to engage the industrious application of a life-time. But we agree with Dr Kidd in thinking that the man who can give a rational explanation of the origin of hair patterns has solved the fundamental problems of evolution. Nowhere are manifest and complex *adaptations* to be seen and studied so readily as on the surface of the vertebrate body—whether it be the arrangements of scales on fishes, feathers on birds, hairs on mammals, or the flexure lines on the palms and soles; all are developed in the young to answer exactly to the movements of the fully grown body and the habits of the living animal. For Dr Kidd there is only one possible way in which such adaptations

could arise—by inheritance of effects produced in the adult or growing body by movement and posture.

His exact position—as well as the humour and gentleness of his style—may be best illustrated by the following passage:

"It will be remembered that a single example was given of a short-haired dog in which its common habit of lying was associated with a definite pattern of hair. This introduces and illustrates the very wide conception of a moulding process undergone by an organism. It is one familiar to biologists....I therefore claim nothing new when, with the temerity of certain persons treading where others are said to fear to do so, I invent an inclusive term and propose to call the two fundamental factors of organic evolution—Plasto-diēthēsis, in which the conceptions of mould (i.e. Lamarckism) and sieve (i.e. natural selection) are included and hyphenated....It has at any rate the merit of having a meaning clear to all friends and opponents alike of Lamarckism. It will be observed that the two words are placed in what I take to be their natural order as expressive of the Alpha and Omega of the story of organic evolution....So the banns between Lamarck and Darwin are published and not for the first time of asking."

Therein Dr Kidd states the result of all his labour—that use and wont mould the animal body and produce its pattern and that the suitable patterns are selected and survive. Whether his readers be followers of Weismann or of Lamarck he has them equally on the horns of a dilemma. For if they are Lamarckists, where is the machinery which transfers the effects of use—wont to the ova—to the spermatozoa? or if they be Weismannites—how do such complex and exact adaptations arise? Perhaps a fuller knowledge of the mechanism of growth and development may solve the conundrum of ages and show that both Lamarck and Weismann were wrong and also that both were right.

This at least is true; Dr Walter Kidd has tabulated and put at the disposal of his biological colleagues a great series of new observations which will materially help in getting at the nature of the machinery of evolution.